

## Holoplanktonic Mollusca (Gastropoda) from the Gulf of Aqaba, Red Sea and Gulf of Aden (Late Holocene-Recent)

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**Abstract.** Fifteen bottom samples, two from the Gulf of Aqaba, twelve from the Red Sea proper and one from the Gulf of Aden, were analysed qualitatively for holoplanktonic Mollusca. The basic material yielded 43 taxa (14 Heteropoda, 1 Janthinidae, 20 Euthecosomata, 4 Pseudothecosomata and 4 Gymnosomata). Eighteen species are distributed all over the Red Sea (9 of them also in the Gulf of Aqaba), another 16 are present only in the southeastern part of the Red Sea, and 10 species were exclusively found in the Gulf of Aden sample. The presence of several further species in the Red Sea (1 heteropod, 4 janthinids, 1 thecosome, 2 pseudothecosomes, 3 gymnosomes and 1 nudibranch) is assumed on the basis of literature data or unpublished observations. Northward increasing salinity is considered to be the main cause for the differences in occurrence. Although all material studied originates from bottom samples, all species are considered to form part of the living holoplanktonic mollusc stock, judging on the presence of well-preserved specimens. Only epi- and mesopelagic species were found. Bathypelagic species are absent. Predominantly based on SEM-imaging additional data on morphology of especially the Heteropoda is given. Taxonomical and/or nomenclatural notes are added for several species.

**Key Words:** Holoplanktonic Mollusca, Holocene, distribution, systematics, Gulf of Aqaba, Red Sea, Gulf of Aden.

### INTRODUCTION

The Red Sea (al-Bahr al-Ahmar, in Arabic language) is the world's northernmost tropical sea, situated in between the NE part of the African continent and the Arabic peninsula. Its length is approximately 1900 km, maximum width is around 350 km. In the NW the Red Sea is subdivided by the Sinai Peninsula into two bights, the western, relatively shallow (~75 m) Gulf of Suez, leading through the Suez Canal to the Mediterranean Sea, and the eastern, much deeper (~1850 m) Gulf of Aqaba [also referred to as Gulf of E(i)lat]. In the SE the relatively narrow (~35 km) Bab el-Mandab Strait connects the Red Sea with the Gulf of Aden and the Arabian Sea, which form part of the Indian Ocean.

Sea depth of the Red Sea proper amounts to over 2400 m in the central part, but is only ~137 m near the southern passage to the Gulf of Aden (Hanish Sill shallows). An isolated position and high temperature within tropical climate, with an average surface water temperature in the north of 26°C, in the south of 30°C (but rapidly decreasing to c. 22°C at a 'thermohalocline' at 100 m sea depth, Weikert, 1982, fig. 2), causing high evaporation, and lack of discharging rivers cause a hypersaline environment (salinity northward to over 40‰), considerably higher than that in the Gulf of Aden and the Indian Ocean (approximately 35‰). High temperature and salinity in the intermediate water column, together with reduced oxygen contents and

lack of food explain the absence of Red Sea bathypelagic species (Weikert, 1982; Hemleben et al., 1996).

Main currents in the Red Sea are influenced by monsoons (Baars et al., 1998). As a result of the wind system, surface currents flow from the Indian Ocean into the Red Sea during winter and the other way around in summer. Surface and nutrient-rich mid-level currents flow in opposite direction, resulting in an outflow of nutrients from the Red Sea during winter and its enrichment during summer (most data from Siddall et al., 2004; and Saudi Geological Survey, 2006). Sediment supply into the Red Sea is mainly by desert dust, transported by strong winds (NASA, 2006).

Geologically the Red Sea is a young (Oligo-Miocene) structure, originated as part of the Great Rift System, as a result of which the Arabian peninsula separated from the African mainland. The Red Sea was never part of the Tethyan Ocean.

An initially existing connection with the Mediterranean was lost in the Middle Miocene (Boswerth et al., 2005, fig. 11). During the Pliocene the connection with the Mediterranean was restored. Sea level fall during the Pleistocene isolated the Red Sea from the Mediterranean as well as from the Indian Ocean, afterwards only the southern connection was restored. During the last glaciation maximum, holoplanktonic organisms (nannoplankton, foraminifera and molluscs,

apart from the pteropod *Creseis* 'acicula' = *C. clava*) did not survive the increasing salinity (>55‰) in the Gulf of Aqaba and the northern part of the Red Sea (Almogi-Labin, 1982 and in litt., 2006). Afterwards, the one and only source of species immigrating into the Red Sea is the southern connection with the Indian Ocean, through the Bab-el-Mandab Strait. It seems that the Gulf of Aqaba was continuously connected during the last 150 kA with the Red Sea and the latter with the Gulf of Aden (Reiss et al., 1984).

At present, immigration of mollusc species from the Mediterranean through the Suez Canal, especially for holoplanktonic molluscs, can be neglected, as the main migration stream seems to be from the Red Sea into the Mediterranean (so-called Lessepsian species). Also, holoplanktonic molluscs are most probably not capable of surviving transportation through the shallow canal.

Thus, the Red Sea holoplanktonic mollusc fauna can be considered a young (holocene) assemblage, originated completely by immigration from Indian Ocean stock.

The extant overall Red Sea mollusc fauna is very rich and diverse in species, due to the presence of a wide variety of environments (as e.g., a complex reef ecosystem). Dekker & Orlin (2000) listed no less than 1765 species by name and referred to a large number of as yet unidentified further species. Holoplanktonic Mollusca from the Red Sea have been referred to in a number of papers, but an up to date overview or systematic revision is not available yet from this area. The recent inventory of Dekker & Orlin includes a number of holoplanktonics (Heteropoda, Atlantidae: 5 species; Janthinidae: 5 species; Thecosomata, Limacinae: 3 species; Cavoliniidae: 9 species; Desmopteridae: 1 species; Gymnosomata, Pneumodermatidae: 1 species). It should be realised, however, that these references are predominantly concentrated from scattered literature resources and are not necessarily based on actual observations of these authors themselves.

#### Abbreviations:

NNM	Nationaal Natuurhistorisch Museum <i>Naturalis</i> , Leiden, The Netherlands.
RGM	Nationaal Natuurhistorisch Museum <i>Naturalis</i> , Leiden, The Netherlands, Palaeontology Department; formerly Rijksmuseum van Geologie en Mineralogie.
SMF	Senckenberg Museum, Frankfurt am Main, Germany.
ZMA	Instituut voor Systematiek & Populatiebiologie, Zoologisch Museum, University of Amsterdam, Department of Malacology.
A	long diameter of atlantid species (Janssen, in press, text-fig. 6).

H	shell height.
W	shell width.

## MATERIALS AND METHODS

Fifteen bottom samples, predominantly from deep water (range 56–2120 m) and reasonably well-spread over the entire length of the Red Sea (Text-fig. 1), were analysed qualitatively for holoplanktonic Mollusca. Eight of these were donated by Dr. Frank P. Wesselingh, who joined a Meteor Red Sea and Gulf of Aden collecting trip in 1995. Samples from the same trip were described and analysed by von Rützen-Kositzkau (1999), who gave extensive additional information, especially on the benthic mollusc material. A further series of 5 Red Sea samples, collected in 1981 (1 sample Valdivia 29) and 1987 (4 samples Meteor 5), was donated by Dr. Ronald Janssen (SMF) in 1996. Two samples from the Gulf of Aqaba were made available by Dr. Ahuva Almogi-Labin (Geological Survey of Israel, Jerusalem, Israel). Locality data of these samples are summarised in Table 1. Sample locations are given in Text-fig. 1.

Most samples were collected by means of box cores that take a bottom sample to a depth of 0.50 m or (usually) less of the sea bottom sediments. The age of such box core samples, as discussed by von Rützen-Kositzkau (1999, p. 49), is no more than maximally ~6 kA (usually less) and can therefore without exception be indicated as 'Late Holocene to Recent.' Such samples, of course, give no information whatsoever on seasonal fluctuations in the holoplanktonic mollusc stock. They just indicate which species occurred at the sampling sites during the last few thousand years. As quite fresh specimens were present for all species, it may be safely assumed that they do occur in the extant assemblages, occurring in the water columns over the sampled sites.

Samples taken and donated by Frank Wesselingh were washed aboard ship on a 120 µm mesh and included small sediment samples. The Senckenberg samples were obviously sieved on a 500 µm mesh and therefore the smallest species and specimens are absent (as e.g., Gymnosomata larval shells). The Gulf of Aqaba samples were received as picked material. One of them contained only specimens >1 mm.

All samples were analysed qualitatively after being separated in sieving fractions of 2000, 1000, 500, 300, 200 and 100 µm. Isolating the smallest specimens (under 200 µm) was frequently hampered by the presence of overwhelming numbers of (mainly planktonic) Foraminifera, which made concentrating the tiny mollusc specimens laborious and very time-consuming. Therefore the coarser three or four fractions usually were inspected completely, the finer ones only partially, until no further species were found. This method gives





Figure 1. Location of samples (compare Table 1).

Table 1  
Sample data (localities arranged from NW to SE, compare Text-fig. 1).

Nr	Locality	Coordinates	Leg.	Station	Sea depth	Date
1	Gulf of Aqaba	off Elat city	unknown	unknown	320 m	unknown
2	Gulf of Aqaba	Geziret Fara'oun 29°30'N;? E	unknown	unknown	380 m	unknown
3	Red Sea	27°41'N; 34°35'E	FS Meteor 31/2	unknown	1040 m	00.02.1995
4	Red Sea	26°44.97'N; 35°02.02'E	Valdivia 29	746 KG 873	1377 m	09.03.1981
5	Red Sea	26°14.477'N; 35°21.033'E	FS Meteor 31/2	DRZ dredge	1146 m	00.02.1995
6	Red Sea	22°35.2'–22°24.8'N to 36°45.9'–36°46.2'E	FS Meteor 5	85	772–779 m	07.02.1987
7	Red Sea	20°57.7'N; 37°25.7'E	FS Meteor 31/2	GKG 93-3	685 m	23.02.1995
8	Red Sea	20°57.5'N; 37°22.1'E	FS Meteor 31/2	GKG 93-10	56 m	23.02.1995
9	Red Sea	19°35.0'N; 38°40.0'E	FS Meteor 5	183 Ku	2120–2119 m	28.02.1987
10	Red Sea	19°33.2'N; 37°24.5'E	FS Meteor 5	196 KG	757 m	28.02.1987
11	Red Sea	19°06.3'N; 38°36.6'E	FS Meteor 31/2	GKG 100-1	393 m	27.02.1995
12	Red Sea	18°32.9'N; 38°59.4'E	FS Meteor 5	unknown	431 m	23.02.1987
13	Red Sea	17°21.7'N; 40°01.3'E	FS Meteor 31/2	MC 101-1	475 m	28.02.1995
14	Red Sea	15°33.0'N; 41°41.1'E	FS Meteor 31/2	MC 102-1	583 m	28.02.1995
15	Gulf of Aden	12°22.8'N; 44°31.5'E	FS Meteor 31/2	GKG 105-3	321 m	04.04.1995

only scant information on the relative abundancy of species, the smaller forms always being underrepresented, but the numbers of specimens included in the collection (as given in Table 2) give sufficient clue in this respect.

Most material is included in the RGM collection of fossil holoplanktonic molluscs, sample 2 is housed in the Geological Survey of Israel. Registration numbers are: sample 1: RGM 540.338–540.345; sample 3: RGM 540.141–540.162; sample 4: RGM 540.163–540.190; sample 5: RGM 540.191–540.206; sample 6: RGM 517.980–518.000 and 540.135–540.140; sample 7: RGM 539.867–539.899, 540.207; sample 8: RGM 539.900–539.915; sample 9: RGM 540.080–540.111; sample 10: RGM 540.112–540.134; sample 11: RGM 540.021–540.054; sample 12: RGM 540.055–540.079; sample 13: RGM 539.960–539.993; sample 14: RGM 539.994–540.020; sample 15: RGM 539.916–539.959. All illustrated specimens separated from these samples are registered with nrs RGM 540.347–540.464.

Benthic mollusc specimens were transferred to Mr. Robert G. Moolenbeek (Zoölogisch Museum, Universiteit van Amsterdam, dept. of Malacology, Amsterdam). Teleostei otoliths found in many samples are in the collection of Mr. Kristiaan Hoedemakers (Mortsel, Belgium).

Preservation of the planktonic mollusc specimens varies from crystal clear to opaque or completely white because of recrystallisation or early stages of dissolution. In the four northwesternmost Red Sea samples (nrs 3–6), however, part of the material, sometimes even more than half the number of specimens, shows distinct dissolution of the aragonite and specimens are preserved as internal calcitic moulds, with or without their shells preserved.

Holoplanktonic molluscs (heteropods, janthinids and pteropods), concentrated from the 15 available samples, are specified in Table 2. Most species, especially so the pteropods, are well-known and sufficiently described in the existing literature, but notes on distribution, systematics and/or morphology are added below.

All SEM-images were made by the author, using the Jeol JSM-6480 LV instrument of NNM. The photographs of Plates 20–21 were kindly made by Mr Frank P. Wesselingh, with a Nikon DS-SM camera.

## SYSTEMATIC PART

As synonyms for most taxa only the first valid description is given, as well as a more recent reference to a paper in which the taxon is described and well-illustrated. Extensive synonymy is to be found usually in van der Spoel (1967, 1976). For the Atlantidae some more attention is paid to the morphology of juvenile specimens, especially also by SEM-images. In particular their protoconchs are still insufficiently known, although in most cases indispensable for the recognition of the species.

Phylum Mollusca Linné, 1758  
Class Gastropoda Cuvier, 1797

Note—Classification of Gastropoda, especially above the rank of superfamily, is in a 'currently very active phase of reevaluation,' as Bouchet & Rocroi (2005, p. 4) put it. To prevent the impression that the present author has a pronounced opinion on higher classification only ranks of superfamily and lower are given here.

Superfamily Pterotracheoidea Rafinesque, 1814 [= Heteropoda Lamarck, 1812 (partim); Carinarioidea de Blainville, 1818]



Table 2

Holoplanktonic mollusc distribution in the Gulf of Aqaba (samples 1–2), Red Sea (samples 3–14) and Gulf of Aden (sample 15). Numbers of specimens per sample locality (m = >50 specimens).

Species	Sample														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Heteropoda															
<i>Atlanta echinogyra</i> Richter, 1972	—	—	—	—	—	—	—	—	4	1	32	—	—	10	10
<i>Atlanta frontieri</i> Richter, 1993	—	—	—	—	—	—	—	—	—	—	10	—	—	4	14
<i>Atlanta fusca</i> Souleyet, 1852	—	—	23	m	5	m	21	6	50	26	m	m	29	—	3
<i>Atlanta helicinoides</i> Souleyet, 1852	—	—	34	m	6	5	47	3	39	13	m	40	m	5	16
<i>Atlanta inclinata</i> Souleyet, 1852	6	10	m	m	m	m	m	15	m	m	m	m	m	10	20
<i>Atlanta lesueuri</i> Souleyet, 1852	—	—	—	—	—	—	—	—	39	13	m	35	m	m	19
<i>Atlanta oligogyra</i> Tesch, 1906	—	—	48	m	17	30	m	10	m	36	m	m	m	—	10
<i>Atlanta plana</i> Richter, 1972	—	—	—	1	—	12	m	—	m	m	m	m	m	m	m
<i>Atlanta turriculata</i> d'Orbigny, 1836	—	—	3	13	1	1	39	1	10	2	23	26	20	6	33
<i>Oxygyrus keraudreni</i> (Lesueur, 1817)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Carinariidae sp. 1	—	—	—	—	—	—	—	—	—	—	1	—	3	—	18
Carinariidae sp. 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Carinariidae sp. 3	—	—	—	—	—	—	—	—	—	—	2	—	5	—	19
<i>Pterotrachea coronata</i> Niebuhr, 1775	Red Sea, from literature data														
<i>Firolida demarestia</i> Lesueur, 1817	—	—	—	—	—	—	m	5	6	—	m	4	m	m	m
Janthinidae															
<i>Janthina exigua</i> Lamarck, 1816	Gulf of Aqaba, from literature data														
<i>Janthina janthina</i> L., 1758	Red Sea, from literature data														
<i>Janthina umbilicata</i> d'Orbigny, 1840	Red Sea, from literature data														
<i>Janthina</i> sp.	—	—	—	7	—	—	1	—	—	—	18	—	4	—	8
<i>Recluzia erythraea</i> Jickeli, 1882	Red Sea, from literature data														
Thecosomata, Euthecosomata															
<i>Heliconoides inflata</i> (d'Orbigny, 1836)	5	m	m	m	m	m	m	m	m	m	m	m	m	m	m
<i>Limacina bulimoides</i> (d'Orbigny, 1836)	—	1	m	—	m	—	m	—	50	6	m	50	40	6	m
<i>Limacina trochiformis</i> (d'Orbigny, 1836)	—	17	24	—	18	7	m	m	29	8	m	25	m	38	m
<i>Creseis chierchiae</i> (Boas, 1886)	—	—	—	—	—	—	5	—	4	2	14	5	9	6	14
<i>f. constricta</i> Chen & Bé, 1964	—	—	7	16	1	13	m	30	m	m	m	m	m	m	m
<i>Creseis clava</i> (Rang, 1828)	19	31	m	m	m	m	m	35	m	m	m	m	m	m	m
<i>Creseis conica</i> Eschscholtz, 1829	—	—	1	—	—	—	m	—	30	28	50	m	m	25	m
<i>Creseis virgula</i> (Rang, 1828)	5	7	m	m	m	m	m	70	m	m	m	m	m	12	m
<i>Hyalocylis striata</i> (Rang, 1828)	—	—	m	—	7	li	m	—	19	17	m	m	m	22	m
<i>Styliola subula</i> (Quoy & Gaimard, 1827)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
<i>Clio (Bellardichio) cuspidata</i> (Bosc, 1802)	—	—	—	—	—	—	—	—	—	—	—	literature data			29
<i>Clio (Clio) convexa cyphosa</i> Rampal, 2002	24	21	m	m	m	m	m	m	m	m	m	m	m	m	m
<i>Clio (Clio) pyramidata f. lanceolata</i> (Lesueur, 1813)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Cavolinia globulosa</i> (Gray, 1850)	southern Red Sea, literature data														
<i>Cavolinia uncinata</i> (Rang, 1829)	7	—	3	12	—	m	8	—	11	2	15	m	m	5	6
<i>Diacavolinia angulata</i> (Souleyet, 1852)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Diacavolinia flexipes</i> van der Spoel et al., 1993	1	—	1	3	—	28	14	—	m	6	36	m	16	11	m
<i>Diacavolinia longirostris</i> (Blainville, 1821)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9
<i>Diacavolinia</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	7
<i>Diacria erythra</i> van der Spoel, 1971	m	34	m	m	m	m	m	31	m	36	m	m	m	m	m
<i>Diacria quadridentata</i> (Blainville, 1821)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
<i>Diacria trispinosa</i> (Blainville, 1821)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3p
Cavoliniidae sp.	—	3	—	m	3	—	24	—	—	—	m	13	m	m	13
Thecosomata, Pseudotheosomata															
<i>Cymbulia sibogae</i> Tesch, 1903	southern Red Sea, literature data														
<i>Cymbulia</i> sp. 1	—	—	3	40	—	—	14	2	1	—	27	—	40	1	5
<i>Cymbulia</i> sp. 2	—	—	—	—	—	—	19	2	—	—	1	—	3	—	—
<i>Desmopterus papilio</i> Chun, 1889	southern Red Sea, literature data														
<i>Peraclis moluccensis</i> Tesch, 1903	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
<i>Peraclis reticulata</i> (d'Orbigny, 1836)	—	—	m	m	m	m	m	1	40	40	m	31	15	—	8

Table 2  
Continued.

Species	Sample														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Gymnosomata															
Gymnosomata sp. 1	—	—	—	—	—	—	43	—	5	—	36	7	m	1	8
Gymnosomata sp. 2	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Gymnosomata sp. 3	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
Gymnosomata sp. 4	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—
Gymnosomata Typ I <i>sensu</i> Kunz, 1996							Red Sea, literature data								
Gymnosomata Typ IIa <i>sensu</i> Kunz, 1996							Red Sea, literature data								
Gymnosomata Typ IIb <i>sensu</i> Kunz, 1996							Red Sea, literature data								
Nudibranchia															
<i>Glaucus atlanticus</i> Forster, 1977							southern Red Sea, K. Bandel (in litt.)								
incertae sedis															
veliger larvae?	—	—	10	—	—	—	m	9	9	—	m	—	m	m	15
'beaked larva' <i>sensu</i> van der Spoel & Newman, 1990	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—

## Family Atlantidae Rang, 1829

Notes—Identification of Atlantidae species solely on shell characteristics remains hazardous. In several papers the importance of soft part anatomy (eyes, radula, operculum) is stressed and considered of utmost importance for the distinction of species, especially within the so-called 'species groups' [note the very different meaning of this wording, contrary to the same term used in the ICZN Code (1999)]. Still, careful study of especially juvenile specimens (protoconchs-1 and -2) enables recognition of the species beyond doubt in most instances, albeit that application of SEM-images usually is requisite. Specimens with missing apical whorls (which occur frequently in bottom sample material) in most cases cannot be identified with any degree of certainty.

For every species in this family one of the larger specimens is measured, giving the shell's long diameter (A), the shell height (H) and the whorl formula, as developed by Tokioka (1955), see also Janssen (in press, text-fig. 6).

Occurrences and distributions of heteropod species in the Red Sea are still largely unknown, as is clear from van der Spoel's (1976) distribution charts. The one and only heteropod species mentioned by him for the Red Sea is *Pterotrachea coronata* Niebuhr, 1775. Larval shells of that species, or even genus, were not recognised during the present study. This species was also listed by Dekker & Orlin (2000, p. 24), probably based on van der Spoel (1976).

In many atlantid species two main spirals can be distinguished on protoconch-2. One is found in the upper half of the whorls, situated at or near the place where the next whorl will attach. It separates an upper,

subsutural zone, on which further spiral lirae may be present. Sometimes the shell wall is slightly angular at this place, giving the whorl a shouldered appearance. I indicate this spiral here as 'shoulder spiral.' A further spiral is often seen lower on the whorl, separating a middle peripheral and a lower umbilical zone. This spiral develops on the teleoconch whorl into the flange-like keel, and is therefore here called the 'keel spiral.' In some species, however, one or both are entirely absent.

Genus *Atlanta* Lesueur, 1817

Type species—*Atlanta peroni* Lesueur, 1817 (Recent).

*Atlanta echinogyra* Richter, 1972

Pl. 1, figs. 1–3; Pl. 2, figs. 1, 2

1972 *Atlanta echinogyra* n. sp.; Richter, p. 90, figs. 3, 5, 7.

1987 *Atlanta echinogyra* Richter 1972—Richter, p. 182, pl. 1, figs. 5, 6; pl. 2, fig. 14; pl. 4, figs. 31, 32; pl. 5, figs. 36 (as *A. echinogyra*, sic!), 42; pl. 6, fig. 47; pl. 7, fig. 57.

Discussion—This species was only found in small numbers in the southeastern part of the Red Sea and in the Gulf of Aden (samples 9–15). Apparently it is sensitive for increasing salinity and therefore does not reach further to the NW.

The early protoconch whorls are ornamented with a variable number of spirals. The shoulder spiral is distinct, but may be partly covered by the next whorl. Frequently an interrupted line of slightly curved spiral segments is seen just below the shoulder spiral (Pl. 1, fig. 2a, b). The peripheral zone of the protoconch whorls is covered with regularly spaced spiral lirae



(Pl. 1, fig. 2a; Pl. 2, fig. 1). The keel spiral is weak or indicated as a slight angularity on early whorls, developing more strongly on later whorls. The base of the adult shell (Pl. 1, fig. 4) shows very fine growth-lines only. The complete protoconch, nucleus included, is covered with an extremely fine granulation (visible at magnification  $c. \times 2k$ , Pl. 1, figs. 2b, 3b). The spiral ornamentation on the subsutural whorl part of the protoconch is more weakly developed than in the specimen illustrated by Seapy (1990, fig. 8E–H).

Measurements of a large specimen (sample 15):  $A = 1.72$  mm,  $H = 0.57$  mm, whorl formula 1:0.29:0.17.

*Atlanta frontieri* Richter, 1993

Pl. 11, figs. 1–3

1993 *Atlanta frontieri* n.sp. Richter, p. 192, pl. 1, fig. 3; pl. 2, fig. 7, pl. 3, fig. 9, pl. 4, figs. 18, 21.

Discussion—Only juvenile specimens were found, in the southeasternmost part of the Red Sea and the Gulf of Aden (samples 11, 14 and 15). Richter recorded the species from the Indian and western Pacific oceans.

The protoconch has four whorls, together forming a low cone with concave tangents (Pl. 11, fig. 2a). The subsutural zone has a single spiral just below the suture on the earliest whorls (Pl. 11, figs. 1b, 2b, 3), and is separated by a well-developed shoulder spiral, shaped as a lamella (Pl. 11, fig. 3), and situated at or just above the place where the next whorl's suture will attach. In juvenile specimens it is visible that the shell wall is slightly angular at the place of the shoulder spiral (Pl. 11, fig. 2a). The peripheral zone is slightly convex and procured with very thin, regularly distributed spiral lirae in the smallest specimens. The keel spiral is clear, but does not cause an angularity of the shell wall. In just one specimen it can be seen that the whorl expanding rapidly is the fifth (Pl. 11, fig. 1a). These characteristics agree with *A. frontieri*, even if insufficient material is available. Also in this species the nucleus of the protoconch is very finely granulated (Pl. 11, fig. 2c).

Measurements of the largest (but still juvenile) specimen:  $A = 1.22$  mm,  $H = 0.56$  mm (shell height in this specimen is not, as usual, the height of the aperture, as the protoconch's apex still reaches beyond the height of the aperture), whorl formula = 1:0.38:0.22, which also indicates that the shell is still juvenile, with just half a teleoconch whorl present.

*Atlanta fusca* Souleyet, 1852

Pl. 2, figs. 3–5; Pl. 3, figs. 1–3

1852 *Atlanta fusca*, nobis; Souleyet, p. 389, pl. 21, figs. 15–29.

1990 *Atlanta fusca* Souleyet, 1852.—Seapy, p. 123, figs. 6G, 10A–D.

Discussion—*A. fusca* is an easily recognisable species, present in almost all samples of the Red Sea and the Gulf of Aden (except samples 1–2 and 14), sometimes in considerable numbers, even in the northwesternmost samples of the Red Sea. It is absent, however, in the Gulf of Aqaba material (but was recorded from that area by Yaron, 1977: 75). It co-occurs with the less common second species from the same species group, *A. turriculata*, in all samples. Only in the Gulf of Aden (sample 15) *A. turriculata* is more frequent than the present species.

The protoconch is relatively high conical, initially even clearly higher than wide (Pl. 2, fig. 5a). The whorls are covered with an irregular spiral ornament (Pl. 3, fig. 2a), in between which the shoulder and keel spirals sometimes are difficult to distinguish. Especially on the early whorls the spirals show a zigzag-structure (Pl. 3, fig. 1a). In adult specimens the boundary between proto- and teleoconch is distinct and situated at the place where the spiral ornament disappears (Pl. 2, figs. 3b, 4b). In fully grown specimens the spiral ornament is still visible on the umbilical side of the shell (Pl. 2, fig. 4a, b). The nucleus of the protoconch (Pl. 2, fig. 5b; Pl. 3, fig. 2b) and the early whorls (Pl. 3, fig. 1b) are covered with an extremely fine granulation (magnification  $c. \times 2k$ ). The ultimate one third of the teleoconch separates from the penultimate whorl. Most specimens retain their reddish-brown colour.

Measurements of a large specimen (sample 12):  $A = 2.16$  mm,  $H = 1.00$  mm, whorl formula 1:0.32:0.14.

*Atlanta helicinoides* Souleyet, 1852

Pl. 3, figs. 4–6; Pl. 4, figs. 1–5

1852 *Atlanta helicinoides*, nobis; Souleyet, p. 384, pl. 20, figs. 23–30.

1987 *Atlanta helicinoides* Souleyet 1852—Richter, p. 179, pl. 1, figs. 5, 6; pl. 2, figs. 15, 16; pl. 4, figs. 31, 32; pl. 5, figs. 33, 40; pl. 6, figs. 43, 44, 51, 52, 54; pl. 7, figs. 58–60.

Discussion—Specimens of this species were isolated from all Red Sea and Gulf of Aden samples (but not from the Gulf of Aqaba), albeit sometimes in rather low numbers independent from the sampling position. Recorded alive from Red Sea plankton hauls by Bandel et al. (1997, p. 162, fig. 4G–H).

Most of the specimens still possess their original brownish colour, strongest in the larval shell part and on the keel basis. The protoconch has a regular spiral ornament all over the height of the whorl. Above the shoulder spiral, which usually is clearly recognisable (but covered by the suture of the next whorl), the ornament may be slightly weaker. The keel spiral is developed as a slight angularity around the base of the juvenile shell (Pl. 4, figs. 1a, 2) and becomes only more

significant after the boundary with the teleoconch. The spiral ornament of the shell's base is visible on the umbilical side of adult specimens (Pl. 3, fig. 6). The nucleus and early protoconch whorls are covered with an extremely fine granulation (Pl. 4, figs. 1b, 4b, c).

Very characteristic in the present material is the strikingly low keel (Pl. 3, fig. 5) of adult specimens, distinctly lower than in the specimen illustrated by Richter (1987, pl. 1, fig. 5) or even Seapy (1990, fig. 11E) and agreeing better with van der Spoel's (1976, fig. 140a, b) illustration. In several well-preserved Red Sea specimens this low keel shows short radial folds directed backward, whereas in van der Spoel's drawing these folds are perpendicular on the shell's periphery.

Richter (1987), among others, stressed the resemblance of *Atlanta inflata* Souleyet, 1852 and the present species. Still, the differences in height/width-proportions of juvenile shells (compare Richter, 1990, pl. 5, figs. 33, 34 and 37, 38) are significant and cannot be overlooked. Also the adult keel is much wider in *A. inflata* (see Seapy, 1990, fig. 11A). This latter species, however, could not be recognised in any of the samples studied here. Apparently it does not occur in the Red Sea, although the species was mentioned (but not described or illustrated) by Bandel et al. (1997, p. 162).

Measurements of a large specimen (sample 4): A = 1.72 mm, H = 0.72 mm, whorl formula 1:0.28:0.17.

#### *Atlanta inclinata* Souleyet, 1852

Pl. 5, figs. 1–5

1852 *Atlanta inclinata*, nobis; Souleyet, p. 375, pl. 19, figs. 9–15.

1990 *Atlanta inclinata* Souleyet 1852—Richter, p. 261, pl. 1, figs. 3, 4, 10; pl. 2, figs. 15, 16; pl. 3, figs. 22, 26, 30; pl. 4, figs. 32, 37, 39.

Discussion—This is the most abundant atlantid species found in the Red Sea samples, present in most samples in more than 50 specimens. It is only less common in the Gulf of Aqaba, in sample 8 (the shallowest sample, from a sea depth of just 56 m) and in samples 14 and 15, in the southwestern Red Sea and the Gulf of Aden, respectively.

The material studied here is characterised by the possession of a protoconch of 4–4¼ whorls, clearly inclined with respect to the teleoconch's axis. Identification of the species as *A. inclinata* is already apparent because of the size of the shell, reaching to over 6 mm shell width in the largest specimens from the Red Sea. In such large specimens the last complete whorl separates from the preceding one, the space is filled by the keel (Pl. 5, figs. 1, 2). On the protoconch whorls a shoulder spiral is vaguely indicated by a very slight angularity of the shell wall (Pl. 5, fig. 3), whereas the keel spiral is more significant (Pl. 5, fig. 5). The internal radial wall structure of the protoconch whorls, de-

scribed by Richter (1990, p. 261), occurring in the related species *A. inclinata* and *A. tokiokai* van der Spoel & Troost, 1972, could be observed in several fresh specimens with the light microscope, but is of course invisible in a SEM-image. Dissolution of inner shell wall parts, also characteristic for these two species (Richter, 1990, pl. 3, figs. 21, 22), could only be seen in some specimens of which protoconch whorls were broken, as most specimens are insufficiently transparent or filled with matrix.

Measurements of large specimen (sample 5): A = 6.64 mm, H = 2.16 mm, whorl formula 1:0.31:0.07.

#### *Atlanta lesueuri* Souleyet, 1852

Pl. 5, figs. 6, 7; Pl. 6, figs. 1–3

1852 *Atlanta Lesueurii*, nobis; Souleyet, p. 380, pl. 20, figs. 1–8.

1990 *Atlanta lesueuri* Souleyet, 1852—Seapy, p. 118, figs. 5B, 6A, 7A–D.

Discussion—This species is a common constituent of the holoplanktonic mollusc stock in the SE part of the Red Sea and the Gulf of Aden only (samples 9–15). Further to the NW it is completely absent. It was already recorded from the Red Sea by Richter (1986, p. 21).

*Atlanta lesueuri* can only be confused with the other species from the same species group, *A. oligogyra* (see below). Both have a protoconch of just three whorls without any ornament, and a teleoconch rapidly increasing in width. In the former, however, the protoconch whorls are separated by incised sutures (Pl. 6, figs. 2, 3), whereas in the latter the sutures of the early whorls are superficial (Pl. 7, figs. 1–3).

Juvenile specimens of *A. plana* in the present material are easily mistaken for *A. lesueuri*, as the shape of the early whorls is quite similar. In *A. plana*, however, the protoconch has one whorl more and a distinct shoulder spiral is always present. The second and third whorl of that species bear faint spirals on the subsutural zone, sometimes difficultly seen with a normal binocular microscope, but clearly present in SEM-images. A shoulder and keel spiral are hardly or not developed in *A. lesueuri*, the lower one occasionally is visible in juvenile specimens as a very faint line (Pl. 6, fig. 3). In specimens of three or less whorls the peripheral zone of the whorls is flattened, giving the shell a more or less rectangular shape (Pl. 6, figs. 2, 3). In completely adult specimens one third of the body whorl separates from the preceding whorl.

The taxa '*Atlanta Lesueurii*' d'Orbigny, 1836 (presently *Limacina lesueuri*) and '*Atlanta Lesueurii*' Souleyet, 1852 (now *Atlanta lesueuri*) are primary homonyms (ICZN art. 53.3 and 57.2). The junior homonym, however, is not automatically to be replaced, but the



case should be referred to the Commission, for ruling under its plenary powers (ICZN art. 23.9.5) (Janssen & Seapy, in press).

Measurements of a large specimen (sample 12): A = 2.76 mm, H = 1.0 mm, whorl formula 1:0.16:0.07. In the measured specimen the last third part of the body whorl separates from the penultimate whorl.

Richter (1986, p. 22) refers to considerably larger specimens (4 mm), and Souleyet (1852, p. 381) even reported specimens with a 'diamètre antéro-postérieur' of 6 mm, but even in such large specimens only a small part of the last whorl separates from the preceding whorl. The Red Sea specimens clearly remain smaller.

*Atlanta oligogyra* Tesch, 1906

Pl. 6, figs. 4–7; Pl. 7, figs. 1–3

1906 *Atlanta oligogyra* n. sp.; Tesch, p. 54, pl. 8, figs. 14–18.

1990 *Atlanta oligogyra* Tesch, 1906—Seapy, p. 118, figs. 7E–H.

Discussion—*Atlanta oligogyra* is a common species in almost all samples, inclusive of the northwestern-most ones. It is absent, however, in the Gulf of Aqaba and in just one sample (nr 14) from the Red Sea proper. It is less common in the Gulf of Aden sample.

This species is distinguished from *A. lesneuri*, of the same species group, by the very superficial sutures of the earliest whorls (Pl. 7, figs. 1–3). In very juvenile specimens (less than three whorls) the shoulder and keel spirals are absent, or just barely visible as faint lines, without any further ornament being present. The shape of such juvenile shells differs significantly from *A. lesneuri* of the same size, as the peripheral zone is not flattened, but regularly curved (Pl. 7, figs. 1–3). In the largest specimens here too the last whorl separates slightly from the penultimate whorl (Pl. 6, fig. 4).

Measurements of a large specimen (sample 6): A = 2.48 mm, H = 0.96 mm, whorl formula 1:0.15:0.05.

*Atlanta plana* Richter, 1972

Pl. 7, fig. 4; Pl. 8, figs. 1–4; Pl. 9, fig. 1

1972 *Atlanta plana* n. sp.; Richter, p. 90, figs. 4, 6, 8.

1990 *Atlanta plana* Richter—Seapy, p. 120, figs. 3A, B, 6E, 8A–D, 9A, B.

Discussion—*Atlanta plana* is a very common species in the southeastern part of the Red Sea (samples 6 to 14) and is also present in the Gulf of Aden sample. In the more northwestern part it is virtually absent (just one specimen in sample 4). Living specimens were mentioned from the Red Sea by Bandel *et al.* (1997, p. 162).

The protoconch of this species has  $3\frac{1}{4}$  rather convex whorls in a conical shape. The shoulder spiral is

distinctly present (Pl. 8, figs. 2a, 3a, 4) all over the protoconch and disappears after the boundary with the teleoconch. It is also visible in more adult specimens, but at places it can be covered by the suture of the subsequent whorl. Very juvenile shells are slightly angular on the place of the shoulder spiral. The keel spiral is much less distinct, at this place the whorl is gradually rounded. On the subsutural zone of the second and the third whorl two very fine and slightly irregular spiral lirae are present (Pl. 7, fig. 4c; Pl. 8, fig. 3b). These are sometimes difficult to be distinguished under a light microscope. In specimens of less than three whorls the peripheral zone bears regularly spaced spiral lirae (Pl. 8, figs. 2a, 3a, 4), that disappear soon adapturally. Also in this species the nucleus of the protoconch is covered with an extremely fine granulation (Pl. 8, figs. 2b, 3c).

Measurements of a large specimen (sample 10): A = 4.40 mm, H = 1.52 mm, whorl formula = 1:0.26:0.07.

*Atlanta turriculata* d'Orbigny, 1836

Pl. 9, figs. 2, 3; Pl. 10, figs. 1–3

1836 *Atlanta turriculata*, d'Orb.; d'Orbigny, p. 173, pl. 20, figs. 5–11.

1990 *Atlanta turriculata* d'Orbigny—Seapy, p. 123, figs. 5C, 9E, F, 10E–H.

Discussion—This species is absent in the Gulf of Aqaba, but present all over the Red Sea and in the Gulf of Aden (samples 3–15), but usually in rather low numbers. This species was recorded alive from the Red Sea by Bandel *et al.* (1997, p. 162, figs. 4E, F, 5).

The protoconch consists of  $c. 3\frac{1}{2}$  whorls. It is high conical, juvenile shells with this number of whorls (Pl. 10, fig. 3a) are twice as high as wide. The fourth and later whorls expand rapidly (Pl. 10, figs. 1, 2a), resulting in a planispiral adult shell, on which the protoconch protrudes almost as a small cylinder. The shoulder spiral is present from the first whorl onwards as a distinct carina in the middle of the protoconch whorls. It becomes less obvious only on the first rapidly widening whorl (Pl. 10, fig. 1) and after the boundary with the teleoconch. On very juvenile specimens the keel spiral is not very clear (Pl. 10, figs. 1, 3a), but gets stronger on later protoconch whorls (Pl. 10, fig. 2a). The subsutural zone of the protoconch whorls seems to be smooth under a light microscope, but sometimes has an ornament of an irregular spiral (Pl. 9, fig. 2c; Pl. 10, fig. 3a, c). The peripheral zone is ornamented with regularly spaced spiral lirae, frequently in a zigzag-shape. Also the base of the juvenile shell bears spirals, that touch the peripheral ornament at an angle (Pl. 10, fig. 3b). The complete protoconch, nucleus included, is covered with a very fine granulation (Pl. 10, figs. 2, 3). The spiral ornamentation is visible on the umbilical side of adult specimens (Pl. 9, fig. 3a, b). Most

specimens still have their original reddish-brown colour preserved.

Measurement of a large specimen (sample 11): A = 1.62 mm, H = 0.64 mm, whorl formula = 1:0.26:0.12.

Genus *Oxygyrus* Benson, 1835

Type species—*Oxygyrus inflatus* Benson, 1835 = *O. keraudreni* (Lesueur, 1817) (Recent)

*Oxygyrus keraudreni* (Lesueur, 1817)

1817 *A(tlanta) Keraudrenii*; Lesueur, p. 391.

1990 *Oxygyrus keraudreni* (Lesueur, 1817)—Seapy, p. 111, fig. 3E–H.

Discussion—Just a single juvenile specimen was found in the Gulf of Aden sample. The species is absent in all samples from the Red Sea proper and the Gulf of Aqaba.

The shell has a diameter of just 1.12 mm, its height is 0.80 mm. The protoconch ornament of spiral lines is rather worn, but just before the damaged apertural margin the sharp boundary with the teleoconch is well-indicated by the sudden disappearance of the spirals. A peripheral belt is clearly indicated on the body whorl, suddenly widening at the boundary with the teleoconch. The very short teleoconch shell part is smooth.

Family Carinariidae de Blainville, 1818

Genus *incertae sedis*

#### Carinariidae sp. 1

Pl. 11, fig. 4; Pl. 12, figs. 1, 2

Discussion—Protoconchs of Carinariidae sp. 1 were present in the Gulf of Aden sample (18 specimens), but the species does not seem to survive in the southwestern part of the Red Sea (3 protoconchs in sample 13, and just 1 in sample 11). More adult specimens or fragments were not found.

The specimens are easily recognised as a carinariid species, by their peculiar shell form: one and a half time wider than high, with the greatest width above the horizontal midline. The apical part of the shell is very slightly conical, with flat whorls, separated by superficial sutures. All specimens are of an opaque whitish colour, but the nucleus in all specimens is brown. The ornament exists of a subsutural spiral on the first two whorls, on both sides separated by a groove-like structure (Pl. 11, fig. 4b; Pl. 12, fig. 2b), disappearing adaperturally. The upper part of the first whorl in some specimens bears some radiating grooves (Pl. 11, fig. 4b). The base of the shell has distinctly radiating folds starting from the umbilicus and a not very well developed circum-umbilical spiral (Pl. 12, fig. 1a, b). The nucleus of the protoconch is beautifully granulated (Pl. 11, fig. 4b; Pl. 12, fig. 2b), markedly coarser than in the *Atlanta*-species.

Carinariid protoconchs are not very well known yet,

and no sufficiently well-preserved Recent material was available to identify the specimens to species level. None of the four Carinariidae protoconchs illustrated by Seapy & Thiriot-Quévieux (1994, figs. 2–13) resembles the present material completely. Their illustration of *Carinaria japonica* Okutani, 1955 resembles the present specimens most, but differs by more developed radiating lines on the early whorls and a much wider umbilicus.

Measurements of a large specimen (3¼ whorls): H = 0.69, W = 1.06, height of aperture = 0.54 mm.

#### Carinariidae sp. 2

Pl. 12, fig. 3

Discussion—Just a single very juvenile specimen, diameter barely more than 0.3 mm, from sample 15 (Gulf of Aden) differs from the two other Carinariidae types found by the absence of any spiral ornament on the first protoconch whorl. The surface of the nucleus is covered with a nice granulation, the separate elements of which tend to develop to spirals at the end of the first half whorl, towards the rather abrupt boundary with protoconch-2. Radiating riblets appear just behind the nucleus. This little shell might belong to the genus *Pterosoma*, as it basically agrees with the illustration of *Pterosoma planum* Lesueur, 1827 in Seapy & Thiriot-Quévieux (1994, fig. 2). It is too juvenile, however, to be identified with more certainty.

#### Carinariidae sp. 3

Pl. 13, figs. 1–3

Discussion—Carinariidae sp. 3 demonstrates a similar distribution as Carinariidae sp. 1: 19 protoconchs were found in the Gulf of Aden sample, and in addition, just 2 specimens in sample 11, and 5 in sample 13.

The juvenile specimens differ clearly from Carinariidae sp. 1 by their somewhat more flattened apical plane (Pl. 13, fig. 1a), the more convex whorls, separated by incised sutures, a more rounded aperture, and a weaker ornament, with a subsutural spiral and very faint radial lines on the first two whorls. Here too, the nucleus of the protoconch has a similar granulated surface (Pl. 13, fig. 2). In the shape of the shell they resemble *Pterosoma planum*, as illustrated by Seapy & Thiriot-Quévieux (1994, figs. 2–4), but in that species the first whorls have no spiral ornament, and the umbilicus is distinctly wider.

Measurements of a large specimen (3 whorls): H = 0.51 mm, W = 0.76 mm, height of aperture = 0.46 mm.

Family Pterotracheidae Rafinesque, 1814

Genus *Firoloida* Lesueur, 1817

*Firoloida demarestia* Lesueur, 1817



Pl. 13, figs. 4–6; Pl. 14, figs. 1, 2

1817 *Firoloida Demarestia*; Lesueur, p. 39, pl. 2, fig. 1, 1b.

1972 *Firoloida desmaresti* (sic!) Lesueur—Thiriout-Quiévreux, p. 560, pl. 6.

1976 *Firoloida desmaresti* (sic!) Lesueur, 1817—van der Spoel, p. 164, fig. 166.

1997 *Firoloida demarestia*—Bandel et al., p. 164, figs. 4I–K.

Discussion—Larval shells of this species are abundant (with hundreds of specimens in some samples, not all collected) in the southwestern part of the Red Sea and in the Gulf of Aden sample. It is absent in samples 1–6 and 10 (but in several of these the finer fractions yielding this species were absent). The species was mentioned from the Red Sea by Bandel et al. (1997).

Fully grown *Firoloida* specimens are 'naked.' The larval shell is shed at metamorphosis. These tiny little shells resemble very small naticids, are wider than high and have just slightly less than two whorls. Richter (1968, p. 379) found specimens in the Gulf of Naples (Mediterranean) with 2½ whorls. There is a clear boundary (in many specimens developed as a ridge, Pl. 13, fig. 6a, b) between the relatively voluminous protoconch-1 and the remaining shell. This embryonic part deviates from the shell's main axis (Pl. 14, fig. 4) and has just somewhat more than half a whorl. The nucleus is granulated (only visible in SEM-imaging, Pl. 13, fig. 4, 5, 6b), also beautifully illustrated by Thiriout-Quiévreux, 1972). The shell part beyond the boundary has faint growth lines.

In one of the specimens the shell's surface is covered with a typical pattern (Pl. 14, fig. 1), possibly representing a kind of bio-erosion, but it could also be a micro-ornament.

Measurements of a large specimen (sample 13) with almost 1¾ whorls: H = 0.47 mm, W = 0.56 mm, height of aperture = 0.32 mm. Franc (1949, p. 141) mentioned a shell width of 0.67 mm.

Note—This species presently usually is indicated with the name *Firoloida desmaresti*, see for instance van der Spoel (1976), Richter & Seapy (1999, p. 643) and many further papers. Tesch (1906, p. 42) referred to no less than 13 taxa within the genus *Firoloida*, among which *F. demarestia* Lesueur, *F. desmarestia* Souleyet, *F. desmarestii* Huxley and *F. desmaresti* Vayssière. In Lesueur's original paper no indication is given after which person the species was named. Therefore, according to ICZN art. 32.5, *F. demarestia* Lesueur, 1817 cannot be considered an incorrect original spelling and must not be corrected. Even not if it is most probable that the name refers to Anselme G. Desmarest, who had been Lesueur's co-author of two previous papers (Kimberling, 2006; with a nice portrait of Lesueur). Van der Spoel (1976, p. 164), who errone-

ously cited Lesueur (1817) as *F. desmaresti*, instead of *F. demarestia*, mixed up things completely by suggesting that the spellings *F. demarestia* in Abbott (1974, p. 135) or *F. demaresti* in Franc (1949, p. 141) were 'corrections of the original misspelling.' Franc, however, did not at all use *demaresti*, both in the title and the text of his paper the name occurs as '*F. Desmaresti*!' Abbott on p. 135 used both *desmarestia* and *demarestia* and one could wonder which of the two should be considered a *lapsus*. Bandel et al. (1997) applied the correct name for this species.

Superfamily Epitonioidea Berry, 1910

Family Janthinidae Lamarck, 1822

Note—Yaron (1977: 75) referred to two samples of *Janthina exigua* Lamarck, 1816, washed ashore on Gulf of Aqaba beaches in 1976. Mienis (1987) and Mienis & Spanier (1987) mentioned specimens of *J. umbilicata* d'Orbigny, 1840 from Rass umm Sid (Sinai) in the Jerusalem collections and to (unchecked?) occurrences of *J. exigua* Lamarck, 1822 and *J. globosa* Swainson, 1822.

Dekker & de Ceuninck van Capelle, 1994 refer to two *Janthina* species from Yemen (Red Sea coast), viz. *J. janthina* and *J. umbilicata*. Henk Dekker's collection also contains a specimen of *J. umbilicata* from the Egyptian Red Sea coast (Dekker, in litt., 2006).

The genus *Rechuzia*, also referred to by Mienis (1987), likewise occurs in the Red Sea, as demonstrated by a specimen of *R. erythraea* Jickeli, 1882 from the Yemen Red Sea coast, in Henk Dekker's collection. *R. erythraea* might be a younger synonym of *R. jehennei* Petit de la Saussaye, 1853.

The occurrence of *Janthina exigua*, *J. janthina*, *J. umbilicata* and *Rechuzia erythraea* in the Gulf of Aqaba/Red Sea-fauna may be accepted as verified, the actual presence of *J. globosa* remains to be confirmed. Larval shells of *J. exigua* from the Red Sea were mentioned by Bandel et al. (1997), but considering the difficult identification of janthinid larval shells also this record has to be checked. In the present samples just unidentifiable remains were encountered.

Genus *Janthina* Bolten, in Röding, 1798

Type species—*Helix janthina* Linné, 1758 (Recent).

*Janthina* sp.

Pl. 14, figs. 3, 4

Discussion—Juvenile specimens or protoconchs were found in 5 samples (nrs 4, 7, 11, 13 and 15).

Apart from a number of isolated protoconchs just three very juvenile specimens beyond protoconch stage were found that cannot be identified to species level. Even small janthinid fragments (not collected) are easily recognisable by their purple colour.

The larval shells are oval shaped, very shiny, one and a half times higher than wide, with about  $3\frac{1}{4}$  whorls, separated by superficial sutures. A slightly reinforced callus covers the umbilicus (Pl. 14, fig. 3a). The apertural margin is simple, not thickened, slightly prosocline in lateral view (Pl. 14, fig. 4a). The last two whorls of the protoconch bear a thickened spiral along the suture, accompanied by three finer spirals just below it. Around the base of the shell about four very insignificant spirals are present. Regularly spaced thin radial grooves bend slightly backward on these spirals (Pl. 14, fig. 3b). Lamellae, as described for *Janthina* sp. by Richter & Thorson (1975, p. 136), are absent. On both the palatal apertural margin and the columellar callus a structure of aragonite scales is seen (Pl. 14, figs. 3c, 4b) at strong magnification. These structures might give the living animal sufficient friction when leaving its shell (I thank Jeroen Goud at NNM for this suggestion!).

The larval shell is obliquely embedded in the first teleoconch whorl, that expands suddenly and has a v-shaped sinus in the growth lines on the middle of the whorl. Such juveniles resemble strongly the drawings given by Laursen (1953, figs. 32, 38) for *Janthina prolongata* (De Blainville, 1822) or *J. pallida* (Harvey, in Thompson, 1840). Bandel et al. (1997, p. 168, figs. 9G–K) illustrated similar janthinid larval shells from the Red Sea, which they identify as *J. exigua* Lamarck, 1816. Their specimens reach only 2.5 whorls.

Measurements of a larval shell with  $3\frac{1}{4}$  whorls (sample 11): H = 0.48 mm, W = 0.38 mm, height of aperture 0.28 mm.

#### Thecosomata

Superfamily Limacinoidea Gray, 1847 (= Euthecosomata, pro parte)

Family Limacinidae Gray, 1847

Genus *Heliconoides* d'Orbigny, 1836

Type species—*Atlanta* (*Heliconoides*) *inflata* d'Orbigny, 1836 (Recent).

#### *Heliconoides inflata* (d'Orbigny, 1836) type B

Pl. 15, figs. 1–2

1836 *Atlanta inflata*, d'Orb.; d'Orbigny, p. 174, pl. 12, figs. 16–19.

2004 *Heliconoides inflata* (d'Orbigny, 1836) type B—Janssen, p. 110, pl. 1, figs. 4–6.

Discussion—*Heliconoides inflata* is by far the most common pteropod in the Red Sea. It is abundantly present in all samples, sometimes in many thousands of specimens. This observation is remarkable, as van der Spoel (1967, fig. 339) mentioned just one occurrence in the Red Sea, indicated by an arrow in his distribution map, suggesting an occurrence beyond its normal distribution pattern. It was, more correctly, indicated

as 'dominant' by Herman (1971, tab. 37.8). Bandel & Hemleben (1995, p. 228, figs. 1C, D, 2) reported on material from the Red Sea, giving additional information on the peculiar reproduction of this species, as earlier described by Lalli & Wells (1973), Wells (1976) and Lalli & Gilmer (1989). Also Barash & Zenziper (1994, p. 57) refer to Red Sea specimens.

Differences in the development of the apertural rostrum led Janssen (2004) to distinguish two types within *H. inflata*. In type A the subperipheral rostrum starts as a weak internal rib on early whorls and protrudes at the apertural margin. In type B a similar rostrum originates from a falciform thickening in the second half of the body whorl. At the thickening the shell is often slightly inflated, but not always.

According to these criteria all the specimens from the Red Sea and the Gulf of Aden seem to belong to type B. Not a single type A specimen was isolated, but many specimens are too opaque to observe presence or absence of an internal peripheral belt in juvenile specimens. All adult specimens with a still more or less transparent shell wall demonstrate the presence of the falciform thickening in the terminal half of the body whorl, but an outward bulging of the shell wall at the place of this thickening is only rarely present.

Specimens in internal mould preservation show the presence of the falciform thickening and the rostrum better than the very fragile specimens in shell preservation. In the latter the extremely thin shell wall above and below the rostrum invariably is broken (Pl. 15, figs. 1, 2), whereas the moulds perfectly show these shell parts. This also demonstrates that the damage of the shells is caused after sampling, by washing, sieving and/or transportation of the residues. The moulds reveal that the specimens reach the sea bottom undamaged. All internal moulds equally belong to type B.

Janssen (2004) also stated that specimens with clear coloration at the base of the shell or at the rostrum invariably belong to type A. This is contradicted by the present material, in which many sufficiently fresh type B specimens have a clear orange-brown colour spot at the beginning of the body whorl, close to the aperture.

Absence of type A specimens in the Red Sea indicates important differences in the geographical distribution of both types, but it is premature to draw taxonomical conclusions from this fact alone.

Measurement of a large specimen in internal mould preservation (sample 4): H = 1.32 mm (= height of aperture), W = 1.92 mm, number of whorls  $3\frac{1}{4}$ .

Genus *Limacina* Bosc, 1817

Type species—*Clio helicina* Phipps, 1774 (Recent).

#### *Limacina bulimoides* (d'Orbigny, 1836)

Pl. 15, figs. 3–5



1836 *Atlauta bulimoides*, d'Orb.; d'Orbigny, p. 179, pl. 12, figs. 36–38.

1977 *Linaciua bulimoides* (d'Orbigny)—Bé & Gilmer, p. 764, pl. 3, fig. 4a–d.

Discussion—This species occurs in far lower numbers than the preceding species. It is rare or absent in some samples and common in others, independent of the sample position. The species seems to be present all over the Red Sea, inclusive of the Gulf of Aqaba (1 specimen in sample 2; see also Yaron, 1977: 76), as well as in the Gulf of Aden. Neither van der Spoel (1967, fig. 342), nor Bé & Gilmer (1977, fig. 10) knew this species to occur in the Red Sea. The former indicated only small patches of this species in the Indian Ocean. The latter authors, however, knew the species from all over the Indian Ocean, inclusive of the Gulf of Aden. Herman (1971) recorded *L. bulimoides* from glacial and post-glacial Red Sea sediments. Almogi-Labin & Reiss (1977) record the species from 'recent and subrecent sediments of the Red Sea.' Almogi-Labin (1982, fig. 3) repeated this, but did not encounter specimens in plankton hauls during the last 30 years in the Gulf of Aqaba and the northernmost Red Sea. It seems that the species disappeared 1–2 kA ago from that area. Its presence in bottom samples can be because of bioturbation (Almogi-Labin, in litt., 2007). The occurrence of fresh specimens in the present samples makes it very probable that this species still is part of the southern Red Sea holoplanktonic mollusc fauna. In the four northwest-ernmost samples the species occurs predominantly as internal moulds, with or without its shell preserved.

Adult specimens are easily recognised by their relatively high shell form and rather flat whorls, compared to *L. trochiformis*. However, very juvenile specimens are more difficult to identify. Almogi-Labin (1982, p. 56) found that they can be easily distinguished, even in specimens <300 µm, by the more depressed suture of the first whorl and the higher spire in *L. bulimoides*, which is acknowledged by the present specimens (compare Pl. 15, figs. 5a and 8–9). The nucleus of this species is covered with an irregular honeycomb micro-ornament (Pl. 15, fig. 5b) that changes on the next whorl to fine, obliquely positioned ridges. This ornament continues until the aperture, but is gradually less strongly developed.

Measurements of a large specimen (sample 12): H = 1.62 mm, W = 0.96 mm, height of aperture 0.76 mm, 6¼ whorls.

#### *Linaciua trochiformis* (d'Orbigny, 1836)

Pl. 15, figs. 6–9; Pl. 16, figs. 1, 2

1836 *Atlauta trochiformis* d'Orb.; d'Orbigny, p. 177, pl. 12, figs. 29–31.

1977 *Linaciua trochiformis* (d'Orbigny)—Bé & Gilmer, p. 769, pl. 3, fig. 2a–d.

Discussion—*Linaciua trochiformis* is a common species all over the Red Sea, inclusive of the Gulf of Aqaba (with abundances in between those of *Helicoides inflata* and *L. bulimoides*), in several samples occurring with hundreds of specimens. As in the case of the foregoing species neither van der Spoel (1967, fig. 341) nor Bé & Gilmer (1977, fig. 15) were aware of its presence in the Red Sea. Almogi-Labin (1982) recorded the species from plankton hauls and from Holo- and Pleistocene Red Sea sediments.

Morphologically this species is easily distinguished by its adult general shell form and convex whorls. Very juvenile specimens, however, have a less convex whorl shape (Pl. 15, figs. 8, 9) and a more superficial suture than juvenile *Linaciua bulimoides* of the same size. The shell's surface has a micro-ornament of spaced oblique ridges (Pl. 15, fig. 6b). The shell wall at the palatal side of the aperture is covered with coarser and more densely placed radial ridges (Pl. 16, fig. 1a) that are composed of close-set granules (Pl. 16, fig. 1b). As in the case of *Jantlina* sp. protoconchs, described above, this may provide the living animal with the necessary friction when leaving its shell.

Measurements of a large specimen (sample 4): H = 1.12 mm, W = 0.99 mm, height of aperture 0.64 mm, 5 whorls.

Superfamily Cavolinioidae Gray, 1850 (= Euthecosomata, pro parte)

Family Creseidae Curry, 1982

Genus *Creseis* Rang, 1828

Type species—*Cleodora* (*Creseis*) *virgula* Rang, 1828 (Recent).

#### *Creseis chierchiae* (Boas, 1886)

Typical form (Pl. 16, figs. 2, 3):

1886 *Cleodora Chierchie* n. sp.; Boas, p. 62, 202, pl. 3, fig. 39ter; pl. 4, figs. 43bis-ter.

1976 *Creseis chierchiae* Boas (*sic!*) – Richter, p. 145ff, figs. 1–2.

f. *constricta* Chen & Bé, 1964 (Pl. 16, figs. 4, 5):

1964 *Creseis virgula constricta*, n. subsp.; Chen & Bé, p. 194, figs. 3d, 4d.

1977 *Creseis virgula* (Rang) *constricta* Chen and Bé – Bé & Gilmer, p. 776, pl. 5, fig. 12a, b.

See Janssen (in press) for extensive synonymy.

Discussion—The typical form of this species occurs in low numbers between the f. *constricta*, in the southeastern part of the Red Sea and the Gulf of Aden (samples 7 and 9–15). Forma *constricta* is present in all samples except those from the Gulf of Aqaba, and is especially abundant in the southeastern part of the Red Sea (samples 7–15). Almogi-Labin (1982, fig. 3; pl. 2, figs. 4, 5) found this species in early Holocene sediments and also Rampal (2002, p. 236) recorded specimens of both forms from the Red Sea.



Frontier (1965) convincingly argued that typical *C. chierchiaie* and '*C. virgula constricta*' were connected in his material with numerous transitional forms and belong to the same species, viz. *C. chierchiaie*. Richter (1976) demonstrated beyond doubt that *C. chierchiaie* is an independent species and not the larval shell part of *Hyalocyclus striata*, as postulated by van der Spoel (1967, fig. 42) and van der Spoel & Dadon (1999, fig. 6.50c).

Both formae are easily recognised between other species of *Creseis* by the typical shape of the protoconch, as well as by the growth pattern of the adult shell, which initially widens rather rapidly, but later on much slower, frequently becoming almost cylindrical in its apertural half. Growth lines and annulations lie slightly higher on the dorsal side of the shell. The f. *constricta* just differs from the typical form by a lack of annulations. Strong magnification ( $\times 1200$ ) reveals the presence of an extremely fine and irregular radial striation (Pl. 16, fig. 5b).

Measurements of a large specimen (sample 10; f. *constricta*): H = 3.34 mm, W (dorsal view) = 0.69 mm, W (lateral view) = 0.66 mm.

#### *Creseis clava* (Rang, 1828)

Pl. 17, figs. 1–2

1828 *C[leodora (Creseis)] clava* N.; Rang, p. 317, pl. 17, fig. 5.

1828 *C[leodora (Creseis)] acicula* N.—Rang, p. 318, pl. 17, fig. 6.

2002 *Creseis acicula* (Rang, 1828)—Rampal, p. 231, figs. 9A–J.

In press *Creseis clava* (Rang, 1828)—Janssen, text-fig. 7; pl. 2, figs. 9a, b, 10a, b; pl. 23, figs. 7a, b, 8.

Discussion—This species is commonly known as *Creseis acicula* (Rang, 1828), see Janssen (in press) for a discussion on the correct name of this species and illustrations of the lectotype.

*Creseis clava* occurs abundantly in all samples. Van der Spoel (1967, fig. 343, as *C. acicula*) did not record the species from the Red Sea area, but Chen & Bé (1977, fig. 22, also as *C. acicula*) included the Red Sea in the distribution pattern. Bandel & Hemleben (1995, p. 231, figs. 4F–I, 5) described early development of this species based on specimens from the Gulf of Aden. Almogi-Labin (1982) found that '*C. acicula*' was the only surviving pteropod species after the glacial salinity maximum. The same author and Barash & Zenziper (1994, p. 59, fig.) mentioned its occurrence in the Gulf of Aqaba.

Mr. Henk Dekker (ZMA; in litt., 2006) reported a mass stranding of this species in September 1993, at Dahab, Gulf of Aqaba, with uncountable specimens washed ashore in a 1 cm thick layer. Living corals had caught numerous *Creseis* specimens, penetrating apex upward from the separate corallites.

The very elongate shell form distinguishes this species easily from other creseids. The most strongly resembling species is *C. conica*, which increases more rapidly in diameter and is usually at least slightly curved.

Measurements of a large specimen (sample 11): H = 10.68 mm, W at aperture = 1.04 mm, W of protoconch = 0.16 mm. Fragments indicate that adults of this species reach more than double this size.

#### *Creseis conica* Eschscholtz, 1829

Pl. 17, figs. 3, 4

1829 *Creseis conica*; Eschscholtz, p. 17, pl. 15, fig. 3.

1977 *Creseis virgula conica* Escholtz (*sic!*), 1829—Bé & Gilmer, p. 748, 776, pl. 5, fig. 13a–c.

Discussion—*Creseis conica* is not rare in the southeastern part of the Red Sea and the Gulf of Aden (samples 7–15), but almost absent in the northwestern part (just one specimen in sample 3, absent in 1–2, 4–6 and 8). Neither van der Spoel (1967, fig. 345) nor Bé & Gilmer (1977, fig. 21) recorded this species from the extant Red Sea fauna.

This species has frequently been misidentified as '*Creseis acicula clava*' (see Rampal, 2002, p. 233; Janssen, in press). It is easily distinguished from *C. clava* by its less elongate, almost completely straight (Pl. 17, fig. 4a) or (usually) slightly and gradually curved (Pl. 17, fig. 3a) shell, with all possible intermediates.

The curved form was described as a new subspecies by Rampal (*Creseis conica falciformis* Rampal, 2002). She admitted that intermediate forms occur, and that both have the same geographical distribution ('vivent aux même latitudes'). The fact, however, that these forms in her material only rarely occur at the same collecting station made her conclude on 'deux entités morphologiquement proches qui doivent répondre à des caractéristiques environnementales différentes' (two morphologically close units that must respond to different environmental features). It is difficult to imagine what ecological diversity within the same water bodies might cause the existence of two subspecies within this holoplanktonic organism. Until more evidence on such differences will be presented I see no reason to maintain two subspecies.

Measurements of a large specimen (sample 13): H = 7.97 mm, W at aperture = 1.18 mm, W of protoconch 0.09 mm.

#### *Creseis virgula* (Rang, 1828)

Pl. 17, figs. 5, 6

1828 *C[leodora (Creseis)] virgula* N.; Rang, p. 316, pl. 17, fig. 2.

1977 *Creseis virgula virgula* (Rang)—Bé & Gilmer, p. 776, pl. 5, figs. 14a–c.

Discussion—This species is present and usually abundant in all samples (1–15). Rampal (1985), however, did not find this species south of 17° N. The Red Sea was not included in van der Spoel's (1967, fig. 345) distribution map of this species. It was, however, mentioned from the Gulf of Aqaba by Almogi-Labin & Reiss (1977, p. 31) and later papers of Almogi-Labin, as well as from the Red Sea by Bandel & Hemleben (1995, p. 233, figs. 6A–C), who described early development in this species.

The shape of the shell is cylindrical, with a distinct dorsal curvature in the apical part. This species has a similar protoconch as *C. conica*, but in very small specimens in which the curvature is not yet present the two can be easily distinguished by the wider apical angle of *C. virgula*. In larger specimens (H over 6 mm) the cylindrical shell part may become slightly flexuous (Pl. 17, fig. 6a).

Rampal (2002, p. 234) introduced a new subspecies, *Creseis virgula frontieri* Rampal, 2002. As distinguishing character she mentioned the larger size (H = 8–11.5 mm), compared to *C. v. virgula* (H = 4–6 mm). The new subspecies was found in a part of the equatorial zone of the African Atlantic.

In the present Red Sea material numerous specimens reach over the size of 6 mm, and several specimens, predominantly those in internal mould preservation of the northwesternmost Red Sea samples, reach distinctly over 10 mm. Especially these larger specimens also show, what Rampal called 'une légère concavité ventrale dans la moitié antérieure,' described above as 'slightly flexuous.' Obviously such size differences belong within the normal range of variability of *C. virgula* and there is no need to distinguish a separate subspecies based on that character. Apparently Rampal's stations are situated at localities with favourable circumstances for the species, where a higher number of specimens can reach large sizes.

Measurements of a large specimen in shell preservation (sample 12): H = 8.38 mm, W at aperture = 1.26 mm, W of protoconch tip = 0.07 mm. Specimens in internal mould preservation (sample 3) reach a size of more than 11 mm, but cannot be measured accurately because of missing protoconchs and/or apertural margins.

Genus *Hyalocylis* Fol, 1875

Type species—*Cleodora (Creseis) striata* Rang, 1828 (Recent).

*Hyalocylis striata* (Rang, 1828)

Pl. 18, figs. 1–5

1828 *C[leodora (Creseis)] striata* N.; Rang, p. 315, pl. 17, fig. 3.

1977 *Hyalocylis striata* (Rang)—Bé & Gilmer, p. 770, pl. 5, fig. 9a, b.

Discussion—This species occurs all over the Red Sea, but in variable numbers. It is common in the northwesternmost Red Sea sample 3, and absent or rare in samples 1–2, 4–6 and 8. More to the southeast it increases in abundance. Van der Spoel (1967, fig. 347) did not include the Red Sea in the distribution pattern of *H. striata*. Bé & Gilmer (1977, fig. 16) indicate it as common, which agrees with my findings. Bandel & Hemleben (1995) also studied Red Sea material of this species (see below).

The transverse ornament of the present species allows an immediate identification. The only other creseid with such annulations is *C. chierchiaie*, which is much smaller, almost straight and far more slender. Strong magnification ( $\times 1000$ ) reveals the presence of an extremely fine longitudinal micro-ornament in between the annulations (Pl. 18, fig. 5b).

Curious is the fact that not a single protoconch of *H. striata* could be recognised in the present samples, not even in the finest fractions. Embryo's of *Hyalocylis striata* were already nicely illustrated by Fol (1875, p. 177, pl. 5, figs. 2–4). The larval shell in these drawings is schematically outlined. Pelseneer (1888, p. 54, pl. 2, fig. 3) gave another schematical representation of the larval shell, basically agreeing with that of Fol.

In spite of these references the larval shell of *Hyalocylis* remained largely unknown, which tempted van der Spoel (1967, fig. 42) to consider *Creseis chierchiaie* to be the larval shell of *Hyalocylis striata*. Richter (1976) convincingly demonstrated this to be erroneous and illustrated a real, but damaged *Hyalocylis* protoconch, fairly well agreeing with the illustrations of Fol and Pelseneer.

Almogi-Labin (1982, p. 58, pl. 1, fig. 16) even referred to 'many young shells which seem to represent the early stages of this species.' Her illustration indeed resembles the ones given by the earlier authors. It remains curious, however, that in the present material (with in several samples abundant adult specimens) not a single protoconch could be traced. An explanation is provided by Bandel & Hemleben (1995, p. 231, fig. 4E). In larval specimens caught alive in the Red Sea they observed 'shrunken and wrinkled remains of a purely organic embryonic shell' and 'the early organic portions of the shell decreased in volume and became wrinkled. This pattern was preserved due to mineral layers added from the inside.' In addition, they observed that 'the apex is usually discarded after some shell growth, and a solid rounded septum in the apical portion of the shell tube is formed.'

Rare specimens with a closed and wrinkled apical portion (Pl. 18, fig. 3a, b), as well as specimens with a septum (Pl. 18, figs. 4, 5a) are indeed found in the



present Red Sea samples. A similar specimen was already illustrated by Tesch (1904, p. 27, pl. 1, fig. 16), who also gave a drawing (fig. 17) of a specimen with its embryonic shell, differing though from Fol and Pelseneer's illustrations. A further specimen was illustrated by Kunz (1996, pl. 11, figs. 4, 5).

By far the most specimens in the present samples, however, do not show these structures, the apical shell part being just a simple opening. In such specimens apparently the larval shell remained organic and present in the living animal (as a necessary protection against infections). After death such an organic structure would disappear rapidly, leaving an empty shell with an apical opening. Obviously, only in cases where the organic tissue already tends to dissolve during life the animal would be forced to close the opening, either by precipitation of calcium carbonate as a consolidation at the inner side of the organic tissue, or by closing the opening with a septum. Apparently calcification of the original protoconch shape occurs only rarely, or is influenced by local circumstances, which would explain the many specimens referred to by Almogi-Labin.

Measurements of a large specimen (in internal mould preservation, sample 3): H = 6.81 mm, W at aperture 2.24 mm, dorso-ventral diameter at aperture = 1.70 mm, number of annulations c. 40.

Genus *Styliola* Gray, 1850

Type species—*Cleodora subula* Quoy & Gaimard, 1827 (Recent).

*Styliola subula* (Quoy & Gaimard, 1827)

1827 *Cleodora subula*; Quoy & Gaimard, p. 233, pl. 8D, figs. 1–3.

1999 *Styliola subula* (Quoy & Gaimard, 1827)—Janssen, p. 18, pl. 3, figs. 7–9 (with neotype designation).

For extensive synonymy see Janssen (1990, p. 32, pl. 5, figs. 13–19, pl. 6, figs. 1–9).

Discussion—This species is absent from all Gulf of Aqaba and Red Sea samples and was only found in just three specimens in the sample from the Gulf of Aden. Almogi-Labin (1982, p. 58, fig. 3) recorded the species as a fossil, mainly from interglacial periods in the Gulf of Aqaba, northernmost and central Red Sea (compare also Almogi-Labin et al., 1998, p. 104).

Family Cliidae Jeffreys, 1869

Genus *Clio* Linné, 1767

Type species—*Clio pyramidata* Linné, 1767 (Recent)

Subgenus *Bellardiclio* Janssen, 2004

Type species—*Clio* (*Bellardiclio*) *cuspidata* (Bosc, 1802) (Recent)

*Clio* (*Bellardiclio*) *cuspidata* (Bosc, 1802)

1802 *Hyalæa cuspidata*; Bosc, p. 241, pl. 9, figs. 5–7.

1977 *Clio cuspidata* (Bosc)—Bé & Gilmer, p. 781, pl. 5, fig. 15a–d.

Discussion—Absent in all samples from the Gulf of Aqaba and the Red Sea, but not rare in the Gulf of Aden (sample 15), from which 29 specimens were isolated. The species was also not recorded from Holocene and Pleistocene samples in the Gulf of Aqaba and the northernmost Red Sea by Almogi-Labin (1982).

Bandel & Hemleben (1995, p. 231) recorded living embryonic individuals of *Clio cuspidata*, caught in the southern Red Sea. As this species is common in the Gulf of Aden larvae obviously are transported northward. None of these, however, was found in the Red Sea samples studied here.

Subgenus *Clio* s. str.

*Clio* (*Clio*) *convexa cyphosa* Rampal, 2002

Pl. 19, figs. 1–4

2002 *Clio convexa cyphosa* n. ssp.; Rampal, p. 240, figs. 16A–E, 23A–B.

In press *Clio convexa cyphosa* Rampal, 2002—Janssen, pl. 3, fig. 4, fig. 2.

Discussion—This species is common in all samples (1–15) investigated, sometimes occurring in thousands of specimens. It is the secondmost abundant species, after *Heliconoides inflata*. Almogi-Labin (1982, fig. 3; pl. 2, figs. 6, 7) listed it (as *Clio convexa*) from plankton hauls and from Quaternary sediments in the Gulf of Aqaba and the northernmost Red Sea. Also Yaron (1977, p. 76) and Barash & Zenziper (1994, p. 59, fig., as *C. pyramidata*) recorded specimens from the Gulf of Aqaba. Rampal (2002) mentioned the species from just one locality in the southeasternmost part of the Red Sea (Bab el Mandeb). Bandel & Hemleben (1995, p. 230, figs. 4C, D) described larval development of this species.

The hump-backed shape of the dorsal side in lateral view (Pl. 19, fig. 2) is the distinguishing character of this subspecies, compared to the nominal subspecies (occurring all over the indo-pacific tropics and subtropics), in which the dorsal profile is gradually curved. *C. c. cyphosa* is the only form occurring in the Red Sea, but it is also present in the Gulf of Aden sample, in which *C. convexa* s. str., however, was not found. So obviously it is not restricted to the Red Sea proper. SEM-imaging (×500) reveals the presence of longitudinal striae at the boundary of protoconch and teleoconch (Pl. 19, figs. 3b, 4b).

Measurements of a large specimen (sample 15): H = 7.14 mm, W at aperture = 4.81, dorso-ventral diameter = 2.99 mm; protoconch H = 0.36 mm, W = 0.24 mm.

*Clio* (*Clio*) *pyramidata* Linné, 1767 forma *lan-  
ceolata* (Lesueur, 1813)



- 1813 *Hyalea lanceolata*; Lesueur, p. 285, pl. 5, fig. 3.  
 1967 *Clio pyramidata* Linnaeus, 1767 forma *lanceolata* Lesueur, 1813 (*sic!*)—van der Spoel, p. 68, fig. 51a–c (with extensive synonymy).

Discussion—Just a single fragmentary specimen was found in the Gulf of Aden (sample 15). Herman (1971, tab. 35.9) and Barash & Zenziper (1994, p. 59), however, mentioned this species (as *Clio pyramidata*) from the Red Sea, probably misidentifications of *Clio convexa*. The species is absent from all Red Sea samples studied for the present paper.

Family Cavoliniidae Gray, 1850

Genus *Cavolinia* Abildgaard, 1791

Type species—*Anomia tridentata* Niebuhr, 1775 (Recent).

*Cavolinia globulosa* (Gray, 1850)

- 1985 *Cavolinia globulosa*. Rampal, p. 267.

Note: The only record of this species is by Rampal, who found it in very low numbers in plankton hauls from the southern Red Sea. The species is absent from all samples studied here.

*Cavolinia uncinata* (d'Orbigny, 1836)

Pl. 20, fig. 1

- 1836 *Hyalea uncinata*, Rang; d'Orbigny, p. 93.  
 1846 *Hyalea uncinata*, Rang—d'Orbigny, pl. 5, figs. 11–15.  
 1969 *Cavolinia mcinata* (Rang, 1829)—van der Spoel, p. 190, fig. 2A, B (with lectotype designation).

Discussion—This large species occurs in most samples (absent only in samples 2, 5 and 8) in reasonable numbers, sometimes even more than 50 specimens. Engel & van Eeken (1962) recorded the species from Eilat (1949). Van der Spoel's (1967, fig. 359) distribution map indicates its presence only in the northernmost Red Sea, inclusive of Gulf of Aqaba and Gulf of Suez. Singer (1994b, p. 8) reported on a mass stranding ('hundreds of millions') of this species in the Gulf of Aqaba.

Van der Spoel (1967, p. 97), probably misled by earlier authors, cited Rang (1829, p. 114) as the original description of *Cavolinia uncinata*, which is incorrect. In Rang's paper the name *Hyalea mcinata* only occurs as an example of a '1er Groupe Globulosæ' within *Hyalea*, without any specific description. D'Orbigny (1836, p. 93) cited '*Hyalea mcinata*, Rang, pl. inéd.' as a synonym, from which I understand that only an unpublished illustration existed at the time, and no description. In his text d'Orbigny (p. 94) wrote: 'Nous sommes le premier à le décrire et à le publier. On voit cependant que son nom est donné par M. Rang. C'est en effet lui qui l'a nommée, dans une monographie inédite. La figure qu'il en donne représente l'animal

avec des appendices latéraux très-longes.' Inevitably, d'Orbigny, 1836 has to be considered the author of *C. uncinata*. The lectotype, however, was selected from Rang's original material (van der Spoel, 1969, p. 191, fig. 2A–B), housed in MNHN. To maintain its status as the lectotype it should be demonstrated that Rang's specimens were syntypes, i.e., that d'Orbigny included them in *H. uncinata*. As apparently d'Orbigny had access to Rang's manuscript it seems very probably that he indeed consulted Rang's material as well. Therefore ICZN art. 74.2 does not apply. Five syntypes of d'Orbigny (1836), now paralectotypes, are available in the collections of The Natural History Museum (London, UK) (Mrs Dr Kathie Way, in litt., 2006).

Van der Spoel (1969, 1971) ultimately subdivided *Cavolinia mcinata* into two subspecies, viz. *C. uncinata uncinata*, with two formae (f. *uncinata* and f. *roperi* van der Spoel, 1969) and *C. uncinata pulsatapusilla* van der Spoel, 1971, also with two formae (f. *pulsatapusilla* and f. *pulsatoides* van der Spoel, 1971). The distribution of *C. mcinata uncinata* is given as Atlantic Ocean (f. *mcinata*), Indian and probably Pacific Ocean (f. *pulsata*) and North Atlantic Ocean (f. *roperi*). For *C. mcinata pulsatapusilla* the distribution is given as Hawakil Bay, Red Sea (f. *pulsatapusilla* s. str.) and 'near Elath,' Gulf of Aqaba (f. *pulsatoides*).

Generally speaking, the distinguishing characteristics between these formae are small and subject to considerable variability (width of aperture, coloration of shell, development of lateral spines, presence of 'hammered sculpture,' curvature of apical spine, etc.) and almost impossible to apply objectively. A quick try out of van der Spoel's (1971, fig. 4) measurements gave following results. Specimens from the Red Sea studied here (sample 6, should be *C. uncinata pulsatapusilla*, according to their locality), with measurements H = 6.3 W = 6.0, fall within the range of *C. uncinata uncinata* f. *uncinata*. Specimens from near the Canary Islands (that would according to their locality belong to f. *uncinata*), with measurements H = 8.7 W = 6.8, fall within the range of f. *pulsata*. Specimens from Indonesia (that would be *C. uncinata mcinata* f. *pulsata*, according to locality), with measurements H = 7.8 W = 5.7, fall indeed within the range of f. *pulsata*. From these results I conclude that also height and width measurements hardly give reliable results. I accept only *C. uncinata* as a species, the various formae I consider normal intraspecific variability.

Measurements of a specimen from sample 6: H = 6.39 mm, W = 5.89, dorso-ventral diameter at mid-height = 3.65 mm; a larger specimen from the Gulf of Aden (sample 15): H = 9.20 mm, W = 7.05 mm.

Genus *Diacavolinia* van der Spoel, 1987

Type species—*Cavolinia longirostris* (de Blainville, 1821) (Recent).

Note—The genus *Diacavolinia* was introduced by van der Spoel (1987, p. 78) for *Cavolinia longirostris* (de Blainville, 1821), at the time including six formae. The main reason to split *Diacavolinia* off from *Cavolinia* was the fact that in the former the protoconch-1 and -2 are thrown off, whereas they are retained in adult specimens of the latter. Van der Spoel et al. (1993) raised the six formae to species level and introduced 16 further *Diacavolinia* species and two formae.

Discriminating the various taxa within *Diacavolinia* relies on unusually small characteristics, necessitating a completely new terminology of shell parts. Van der Spoel et al. (1993) followed the tendency of many other papers of the last decades, i.e., introducing new taxa based on minor characteristics or (frequently insufficient) zoogeographical information. Generally speaking, I am inclined to accept only those species that can be separated on the basis of morphological hiatuses. In cases where gradual changes occur within populations I rather accept intraspecific variability or formae, at the most. Subspecies are to be distinguished only if morphological differences are induced by a different geographical (or stratigraphical; maybe even environmental? See above under *Creseis conica*) distribution. In the case of *Diacavolinia* one would need an enormous world-wide material (which I don't have available) to get a fair impression on the validity of all new taxa. Probably, biologists will obtain much more reliable results by DNA sequencing, eventually. The geographically very restricted material available for the present study is not suitable for a final decision whether or not 'good species' (van der Spoel, 1987, p. 78) are represented.

For a discussion on the larval development of *Diacavolinia* see below, under Cavoliniidae sp.

#### *Diacavolinia angulata* (Souleyet, 1852)

Pl. 20, fig. 2

1850 *Cavolina angulosa*—Gray, 1850, p. 8.

1852 *Hyalæa angulata*, nobis; Souleyet, p. 152, pl. 5, figs. 1–6.

1993 *Diacavolinia angulosa* (Gray, 1850)—van der Spoel et al., p. 143, figs. 18A–D, pl. 2, figs. 22, 23.

Discussion—Just a single specimen was collected from the Gulf of Aden (sample 15). Van der Spoel et al. (1993, fig. 27) recorded the species from the central Indian Ocean and western Pacific. The northwestern-most part of that area comes close to the Gulf of Aden indeed.

The name *Cavolina angulosa* was published by Gray (1850, p. 8) without description, but with reference to an as yet unpublished manuscript (cited as: 'Eydoux & Souleyet, Voy. Bonite Moll. t. 4, f. 1, 6, not described'). The reference clearly points to a manuscript, later published by Souleyet (1852, p. 152, pl. 5, figs. 1–6),

where the species was described as *Hyalæa angulata*, with the vernacular name 'Hyale angulée,' also mentioned by Gray. Obviously Gray had access to or information about Souleyet's manuscript. To be nomenclaturally available, names published before 1931 must be 'accompanied by a description or a definition of the taxon that it denotes, or by an indication' (ICZN, 1999, art. 12.1). In the absence of a description or definition of '*Cavolina angulosa*' in Gray (1850) one may wonder if the reference to 'Eydoux & Souleyet' can be accepted as an indication. But art. 12.2.1 of ICZN clearly states that only a reference to 'a previously published description' can be accepted as an indication. This makes *Cavolina angulosa* Gray, 1850 an unavailable name.

The specimen differs clearly from other *Diacavolinia* specimens in the same sample, especially by the presence of a well-developed 'outer hump,' a notch in the rostrum and by more faintly developed dorsal ribs, with almost invisible lock ribs, nicely agreeing with Richter's (1979, pl. 3, fig. 37) illustration.

Measurements of the only available specimen (sample 15): H = 3.52 mm, W = 3.24 mm, dorso-ventral diameter = 1.60 mm, W of joint = 0.92 mm.

#### *Diacavolinia flexipes* van der Spoel, Bleeker & Kobayashi, 1993

Pl. 20, fig. 3

1971 *Cavolinia longirostris* (de Blainville, 1821) forma *flexipes* n. forma—van der Spoel, p. 16, figs. 15, 16, 19, 21.

1979 *Cavolinia longirostris*, forma *flexipes*—Richter, p. 20, pl. 3, figs. 31–33.

1993 *Diacavolinia flexipes* (van der Spoel, 1971); van der Spoel, Bleeker & Kobayashi, p. 147, figs. 24A–D, pl. 2, fig. 30.

Discussion—This species is present in some specimens in samples 1 and 3 to 8, but is more common in the southeastern part of the Red Sea and in the Gulf of Aden. It is the only *Diacavolinia* species recorded for the Red Sea by van der Spoel et al. (1993, fig. 36). Many earlier authors referred to this species with the name *Cavolinia longirostris*. Barash & Zenziper (1994, p. 58) also refer to specimens from the Gulf of Suez.

*Diacavolinia flexipes*, according to its original description, is especially characterised by its lateral spines being strongly curved dorsally, to even perpendicular to the shells' horizontal axis, and by the absence of a notch in the rostrum. Many specimens in the Red Sea material demonstrate the curved spines distinctly, but in many other shells it is less clear. In fact all transitional forms are present from hardly bent to strongly bent dorsally. Also presence or absence of a notch in the rostrum frequently is unclear, and a matter of taste. This makes a distinction doubtful



from especially *D. longirostris* (de Blainville, 1821), as redefined in van der Spoel et al. (1993, p. 132, figs. 3A, B, pl. 1, figs. 1–4), who also included in *D. flexipes* forms with less strongly bent lateral spines and with a slight notch in the rostrum (van der Spoel et al., 1993, fig. 24C, D). Following its authors I have identified all specimens from the Red Sea proper as *D. flexipes*, but considering the present material I wonder if this taxon should be given higher rank than forma. As stated above, however, the real status of all taxa in the *Diacavolinia*-complex should be (re-)evaluated in a much wider context.

The name *flexipes* was introduced by van der Spoel, 1971 as an infrasubspecific taxon and is therefore not available as a name of the species group (ICZN, 1999, art. 10.2, 45.6.4). Although Richter (1979, p. 20) in his text used '*C. l. flexipes*' it is clear from his further text and from the explanation of his pl. 3 that he interpreted the name '*flexipes*' in an infrasubspecific sense, and therefore ICZN art. 45.6.4.1 does not apply. So, van der Spoel et al. (1993) were the first to validate the name as a taxon of the species group.

Measurements of a large specimen (sample 12): H = 7.14 mm, W = 5.98 mm, dorso-ventral diameter = 3.24 mm, W of joint = 1.00 mm.

*Diacavolinia longirostris* (de Blainville, 1821)

Pl. 21, fig. 1

1821 *Hyalaea longirostris*, Lesueur; de Blainville, p. 81.

1993 *Diacavolinia longirostris* (De Blainville, 1821)—van der Spoel, Bleeker & Kobayashi, p. 132, fig. 3A, B, pl. 1, figs. 1–4.

Discussion—This species, as interpreted by van der Spoel et al. (1993) is not recorded from the Red Sea, but its occurrence in the western Indian Ocean (van der Spoel et al., 1993, fig. 40) makes it probable that it is present in the Gulf of Aden. I selected a number of specimens from sample 15 (= Gulf of Aden), demonstrating the distinguishing characters of this species (notch in rostrum, only slightly curved lateral spines, etc.), but as stated before, it would not have been difficult to separate a number of very similar specimens from the samples identified *D. flexipes* above, from the Red Sea proper.

Van der Spoel et al. (1993) stated that the type material of *D. longirostris* could not be located. They interpret 'typical' *D. longirostris* as 'the taxon that is certainly not described under another name than "*longirostris*.'" In this genus, however, with so many closely resembling taxa and severe identification difficulties, it would have been common sense to designate a neotype for the type species! Also they wrote that the type locality 'is not exactly given, probably it is the Atlantic Ocean,' which is erroneous,

as de Blainville explicitly stated: 'trouvée dans l'Océan Atlantique, 22°9' de latitude.' This, fortunately, agrees quite well with the distribution map in van der Spoel et al. (1993, fig. 40), which includes the latitude of 22°9' (North!) in the western Atlantic.

Measurements of a large specimen (sample 15): H = 6.56 mm, W = 5.81 mm, dorso-ventral diameter = 3.40 mm, W of joint = 1.08 mm.

*Diacavolinia* sp.

Pl. 21, fig. 2

? 1993 *Diacavolinia elegans* n. sp.; van der Spoel, Bleeker & Kobayashi, p. 136, figs. 9A, B, D; pl. 1, fig. 12.

Discussion—Seven specimens were found in sample 15, one further shell was isolated from sample 13.

These specimens differ from the *Diacavolinia flexipes-longirostris*-group by their small size, short rostrum without a notch, and short lateral spines, that are only slightly curved dorsally. Applying the dichotome identification key in van der Spoel et al. (1993, p. 149) leads to the species *D. elegans* van der Spoel et al., 1993, but that species is unknown from the Indian Ocean. In their remarks to *D. elegans* the authors state: 'The present species may be rather easily confused with juveniles of other species. Presence of a fully developed lock mechanism and thickening of the ventral lip rim should be controlled to determine the adult stage of the shell before it can be identified as *D. elegans*.' The lock mechanism, however, is clearly visible in the available specimens, and in most the ventral lip is reinforced indeed. I choose to record this material in open nomenclature instead of applying the name *D. elegans*.

Measurement of a large specimen (sample 15): H = 3.90 mm, W = 3.90 mm, dorso-ventral diameter = 2.03 mm, W of joint = 0.95 mm.

Genus *Diacria* Gray, 1847

Type species—*Hyalaea trispinosa* de Blainville, 1821 (Recent)

*Diacria erythra* van der Spoel, 1971

Pl. 21, fig. 3; Pl. 22, figs. 2, 3

1971 *Diacria quadridentata* (de Blainville, 1821) subsp. *erythra* n. subsp. forma *erythra* n. forma; van der Spoel, p. 5, fig. 6a–c.

1982 *Diacria erythra erythra* Van der Spoel—van Leyen & van der Spoel, p. 102ff.

Discussion—This species is common to abundant in all samples (1–15), the material includes many isolated protoconchs (Pl. 22, figs. 2, 3a, b) as well.

Van der Spoel (1971) introduced *D. erythra* from the Red Sea, as a subspecies of *D. quadridentata*. Apart from the typical form he also distinguished a forma



*crassa* van der Spoel, 1971, which was raised to subspecies level by van Leyen & van der Spoel (1982). These authors considered *D. erythra erythra* to be a 'subfossil' distributed in the Red Sea and western Indian Ocean and *D. erythra crassa* as a Recent endemic of the Red Sea, that may have occurred, in the geological past, also in the west Indian Ocean near Madagascar. Concerning *f. crassa* van der Spoel (1971, p. 7) stated: 'the shell shape resembles that of the other formae of this species it is only an exceptionally large form.'

**Measurements**—In both papers referred to above measurements were used to discriminate between the various taxa, using the parameters 'shell length' (H, in this paper), 'shell width' (W), and the ratio H/W. As both *D. erythra* s.str. and *D. erythra crassa* could be expected in the present material a random sample of hundred specimens (sample 12, c. 300 km NNW of the type locality of *D. erythra*) was measured in the same way (same parameters). Also the dorso-ventral diameter was measured, as well as the distance between the lateral spines and the width of the caudal spine mark, for comparison with numerical data provided by van Leyen & van der Spoel (1982, p. 109, tab. 2).

As obviously shell size was the most important criterion to distinguish *erythra* and *crassa* measurements of H and W are given in Text-fig. 2a. The discriminating boundary of H = 3.12 mm, as given by van der Spoel (1971, p. 6–7), is indicated in that graph, but a clear separation in two groups is not present. According to this parameter twenty specimens would belong to *crassa*, the others to *erythra* s.str.

Shell height compared to the H/W-ratio is given in Figure 2b. Here also the boundary, as given by van der Spoel (1971, fig. 2) is indicated. He found a clear separation between both taxa, but only 7 specimens of *erythra* were measured. Ranges for the H/W-ratio according to his data are 1.19–1.39 for *erythra* and 1.09–1.29 for *crassa*. These ranges, however, are in no way recognisable in my measurements. According to his data a large number of smaller specimens, with H/W-ratio <1.19 would thus belong to *crassa*. In my measurements the specimens that according to shell height would belong to *erythra* s. str. demonstrate a much wider variability than *crassa* and nothing in the distribution points to a separation in two groups, although it is clear that smaller specimens are much more variable in H/W-ratio than larger ones.

Dorso-ventral diameter range, as measured by van der Spoel, was 2.00–2.48 for *erythra* and 2.60–3.32 for *crassa*. As seen in Text-fig. 2c the measured specimens of sample 12 cover a total range of 1.6–2.7, and just three specimens would be sufficiently convex to belong to *crassa*. Additionally, many shells are too flat (below 2.0) even to belong to *erythra* s. str. The overall distribution of the points in Figure 2c, however, gives

no indication of two taxa present. Here the larger specimens just show a slightly wider range of variability in dorso-ventral diameter.

Width between lateral spines was not measured by the authors referred to, but van Leyen & van der Spoel (1982) repeated measurements given by Frontier (1973, p. 256), who measured specimens from near Madagascar. The range of variability found by him is given as 0.85–1.3 mm, whereas the range in my measurements (Figure 2d) is practically double, viz. 1.62–2.26 mm. The distribution curve in the stacked bar graph of Text-fig. 2d is admittedly irregular but a really clear separation is not possible.

Finally, ranges of the width of the caudal spine mark, the place where the larval shell breaks off from the teleoconch, as given by van der Spoel (1971), are 0.90–0.96 mm for *erythra* and 1.04–1.36 mm for *crassa*. The range of the sample (Text-fig. 2e) is 0.84–1.16 mm and most of the specimens fall between the ranges given by van der Spoel. The graph represents a nice, only slightly asymmetrical normal distribution curve.

From all these data I conclude that a separation of *Diacria erythra erythra* and *D. e. crassa* is purely artificial. Therefore, I indicate all specimens as *Diacria erythra*. Just one variable taxon is present in the investigated bottom sample, a result that, for sure, is true for the entire Red Sea population. It might be useful to test the above results on a population of specimens caught alive, as one of the taxa (*erythra* s. str.) was supposed to be a 'subfossil,' but I do not expect this to give spectacular results, as fresh specimens of all sizes are represented in my samples. In addition, the above results basically agree with the findings of Yaron (1978), who studied samples from the Gulf of Aqaba and the northernmost Red Sea.

According to the distribution map in van Leyen & van der Spoel (1982, fig. 8) another species, *Diacria danae* van Leyen & van der Spoel, 1982 should occur in the Red Sea. It was not recognised in the present samples, specimens with a shell height range in between 1.3 and 1.9 mm were not found.

#### *Diacria quadridentata* (de Blainville, 1821)

##### Pl. 21, fig. 4

1821 *Hyalea quadridentata*, Lesueur; de Blainville, p. 81.

1971 *Diacria quadridentata* (de Blainville, 1821) subsp. *quadridentata* (de Blainville, 1821) forma *quadridentata* (de Blainville, 1821)—van der Spoel, p. 4, fig. 5

**Discussion**—Four specimens in sample 15 (Gulf of Aden) differ clearly from the many specimens of *D. erythra* in the same sample by their faintly developed radial ribs on the dorsal shell part and the almost complete absence of transverse striae close to the dorsal

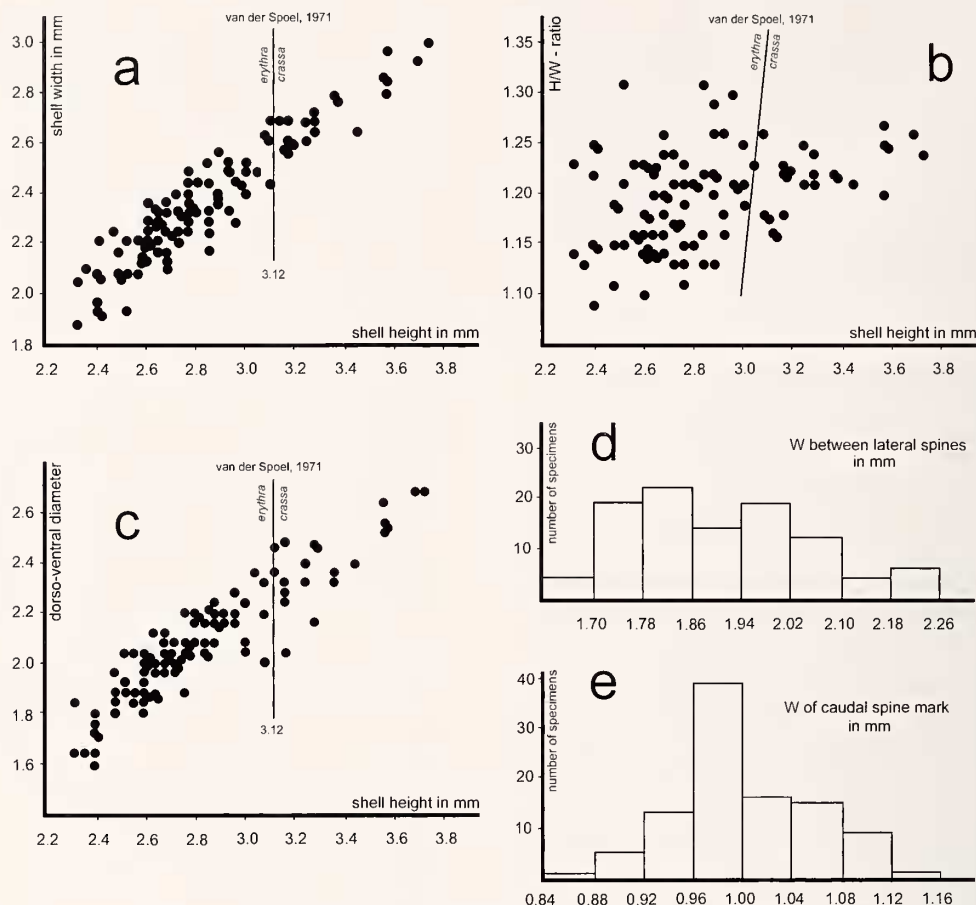


Figure 2. Measurements of 100 specimens of *Diarcia erythra* (sample 12).

margin. Their measurements agree fairly well with the ranges of *D. quadridentata* (s. str.), as given by van der Spoel (1971), H of the largest specimen (3.08 mm) just exceeding the maximum value given by that author (2.9 mm), the three other specimens fit those ranges completely. The Gulf of Aden is not included in the distribution map for this species in van Leyen & van der Spoel (1982, fig. 8), but it is indicated to be present more to the South in the western Indian Ocean.

Measurements of the largest specimen: H = 3.08 mm, W = 2.56 mm, W between lateral spines = 2.24 mm, W of caudal spine mark = 1.12 mm, dorso-ventral diameter = 2.04 mm, H/W = 1.20.

#### *Diarcia trispinosa* (de Blainville, 1821)

1821 *Hyalæa trispinosa*, Lesueur; de Blainville, p. 82.  
 1967 *Diarcia trispinosa* (ms. Lesueur) (Blainville, 1821)—van der Spoel, p. 84, fig. 76a-c.

Discussion—Just three damaged larval shell parts were found in the Gulf of Aden (sample 15). The species is absent in all samples from the Gulf of Aqaba and the Red Sea proper. Bé & Gilmer (1977, fig. 28) include the Indian Ocean (apart from its central part)

with the Gulf of Aden in the distribution pattern of *D. trispinosa*. To Dupont (1979, figs. 9, 10), however, *D. trispinosa* was unknown from the northern part of the Indian Ocean. Herman (1971, tab. 35.8–9) found *D. trispinosa* in Late Glacial and Post-Glacial sediments of the Red Sea. Almogi-Labin (1982, fig. 3) recorded this species from the Gulf of Aqaba and the northernmost Red Sea in cores from the Pleistocene interglacial marine isotope stage 5. The present material indicates its rare presence in the Gulf of Aden, at least during the last few kA.

For a discussion on the validity of the many different taxa presently included in the *Diarcia trispinosa*-group fide Janssen (2004). The present specimens could easily be distinguished from accompanying larval shells of the *D. quadridentata*-group, by the spherical shape of the protoconch-1.

#### Cavoliniidae sp. indet.

Pl. 19, fig. 5; Pl. 22, fig. 1

Discussion—In various samples studied here (see Table 2) juvenile specimens and protoconchs of Cavo-

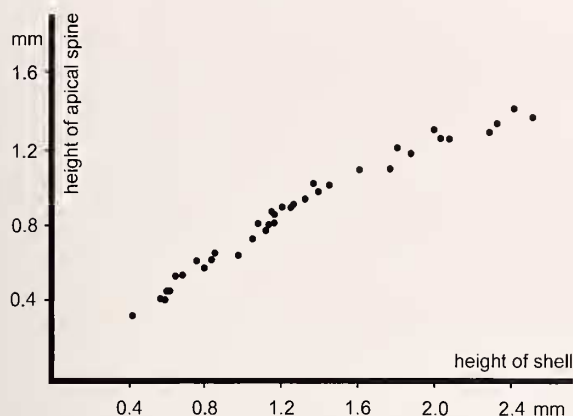


Figure 3. Measurements of Cavoliniidae sp. protoconchs (sample 11).

liniidae are common, undoubtedly belonging to either *Cavolinia uncinata* or *Diacavolinia flexipes*, as these are the only two cavoliniid species recognised. I have measured (Text-fig. 3) a number of such juvenile specimens in shell preservation in the same way as Troost & van der Spoel (1972, p. 226) indicate: apical spine height is the part of the shell posterior of the aperture. Shells were measured in dorsal view, positioning the very fragile specimens on their convex ventral side, with the dorsal apertural margin and the tip of the protoconch in focus. Thirty eight specimens, all with intact protoconch and apertural margin, and in pre-metamorphosis state, were measured.

Troost & van der Spoel found a distinct bimodality in such measurements, concluding on two species, which they identified as *Cavolinia inflexa* (Lesueur, 1813) and '*Cavolinia longirostris*.' Such a bimodality, however, is not found in my measurements, which just show a slight allometric growth, caused by the increasing size of the apertural part of the protoconchs. This might indicate that just one species is represented in this material, or that the larval shells of the two expected species (*Cavolinia uncinata* and *Diacavolinia flexipes*) do not differ in the measured parameters. Larval shells of *C. inflexa* differ clearly in shape from those of '*C. longirostris*': compare Troost & van der Spoel (1972, figs. 4a and 6c), representing specimens of 1.90 and 1.94 mm, respectively. In the former the shell is triangular, with a hardly developed apertural part, in the latter the apertural part is grown out to a half circular shape and these differences cause the bimodality in their graph.

Another Red Sea sample (nr. 3) contains many juvenile Cavoliniidae in internal mould preservation. These specimens have exactly the same shape as the specimens in the measured sample and moreover agree quite well with Troost & van der Spoel's (1993, fig. 6)

drawings of '*Cavolinia longirostris*.' Even on very small specimens in this sample the development of a stronger central and two weak lateral ribs on the dorsal side is visible. This ornament is also present on the measured specimens (compare also Pl. 22, fig. 1), but because of the lustre of the shells more difficult to observe. The internal moulds form together an ontogenetical series distinctly leading to *Cavolinia uncinata*. In the same sample a single juvenile *Diacavolinia* is present, recognisable by the shed larval shell and its joined dorsal and ventral shell walls (Text-fig. 4). In this specimen it can be seen that the radial ribs of the dorsal side start after the point where the joint is formed and that larval shells of *Diacavolinia* will not show this ornament yet. This leads to the unexpected possibility that all larval shells found in the present Red Sea samples belong to *C. uncinata*, and that the protoconch of *D. flexipes* is as yet unknown.

A larval specimen of '*C. longirostris*' with  $H = 2$  mm, identified on the basis of its soft parts, was illustrated by van der Spoel (1967, figs. 230, 231). That specimen shows an almost straight shell, only very slightly curved dorsally, completely different from the specimens illustrated by Troost & van der Spoel (1972, fig. 6a–c) and the question arises if these latter authors did not study juveniles of another, real *Cavolinia*-species, instead of *Diacavolinia*!

Bandel & Hemleben (1995, p. 238, figs. 10A, B, 11A) described the development from eggs produced by mature specimens of *Diacavolinia longirostris*, caught in the Gulf of Aden. They mention the presence of a larval shell and the formation of a septum (when the shell has reached a height of about 4.8 mm) and shedding of the initial part. Interesting is the observation of demineralisation of the teleoconch after shedding, enabling deformation to the adult shell shape, after which the shell will be rapidly remineralised, fixing its new shape.

It must be kept in mind that larval shells may not be calcified at all (van der Spoel, 1967, p. 151), see also above under *Hyalocyclus striata*. If *Diacavolinia* larvae indeed have uncalcified shells (or will be decalcified anticipating shedding and metamorphosis) these will be dissolved in bottom samples, explaining their absence in the samples studied here. There is also another indication of *Diacavolinia* larval shells being uncalcified. In other pteropods shedding their larval shells (such as *Hyalocyclus*, *Cuvierina*, *Diacria*) a calcareous diaphragma (septum) is built to close the opening and invariably the place of fracture is irregular, with small fragments of the larval shell still adhering to the teleoconch (that may only disappear in fully adult specimens). In post-larval *Diacavolinia* there is no or only a very narrow septum, dorsal and ventral shell parts fit together with no opening in between and there is no trace of larval shell fragments adhering at the place of rupture.



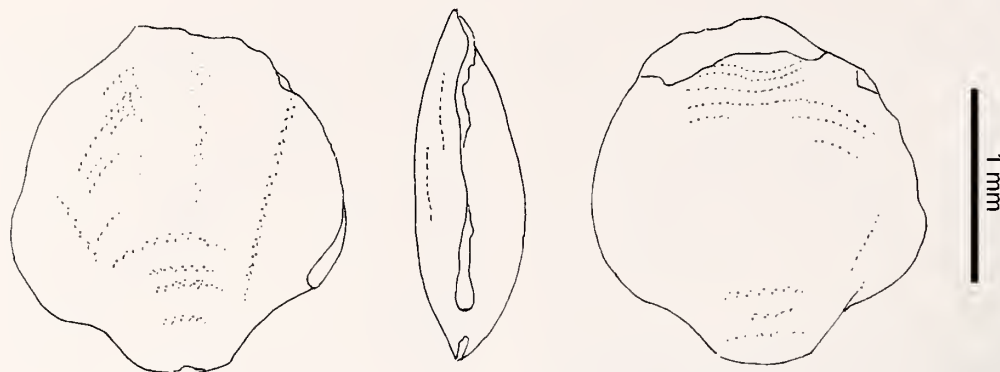


Figure 4. *Diacavolinia flexipes*, juvenile specimen in internal mould preservation (sample 12, RGM 540.157).

Van der Spoel (1987, p. 77) wrote 'In *C. longirostris* the protoconch-1 and -2 are actively thrown off when the shell is nearly full-grown and the opening in the teloconch resulting from this loss is closed by a bending of dorsal and ventral shell sides, which after their bending grow together.' This is at least partly contradicted by two juvenile specimens in the present material, one in extremely fragile shell preservation from sample 11 and one as an internal mould already mentioned above, in sample 3 (Text-fig. 4). Both specimens, H respectively 2.48 and 1.92 mm, already have their protoconchs thrown off, but dorsal and ventral shell parts of the teloconch are still flat, not yet showing the convex shapes of the fully grown specimens. This demonstrates that shedding of the larval part takes place in a rather juvenile state, and certainly not 'when the shell is nearly full-grown.'

Bandel & Hemleben (1995) demonstrated that remineralisation of the shell only takes place after shedding of the larval 'shell' and metamorphosis to the adult shell shape. This would also perfectly explain the almost seamless connection of dorsal and ventral parts after shedding.

Postlarval development of the *Diacavolinia* shell was also extensively described by Richter (1982), but he did not study the protoconch itself.

Superfamily Cymbulioidea Gray, 1840 (= Pseudothe-cosomata)

Family Cymbuliidae Gray, 1840

Note—Two subfamilies within the Cymbuliidae are presently distinguished, viz. Cymbuliinae and Glebinae, the former with one genus, *Cymbulia*, and three species, the latter with two genera, *Gleba* and *Corolla*, with two and five species respectively. Larval shells of *Gleba cordata* Niebuhr, 1776 were nicely illustrated in Kunz (1996, pl. 27, figs. 1–4).

Rampal (1985) recorded two species from plankton hauls in the southern Red Sea, viz. *Cymbulia sibogae* Tesch, 1903 and *Desmopterus papilio* Chun, 1889. It cannot be decided if the two forms described below

belong to these species, as their larval shells are insufficiently known. The two species recorded by Rampal are included in Table 2 as 'literature data.'

Subfamily Cymbuliinae Gray, 1840

Genus *Cymbulia* Péron & Lesueur, 1810

Type species—'Cymbulie Proboscidee' = *Cymbulia proboscidea* Lamarck, 1816 (nomen oblitum) = *Cymbulia peroni* de Blainville, 1818 (nomen protectum).

Note—Van der Spoel (1976, p. 37) wrote 'The name *C. proboscidea* Lamarck, 1816 should have priority; for stability in nomenclature, however, *C. peroni* is still used because correction would now give too many confusion.' By this statement van der Spoel obviously referred to art. 23 of the then valid second edition of the ICZN code. However, he did not, as required, refer 'the case to the Commission for a ruling.'

In the presently valid ICZN code (1999), according to art. 23.9 a ruling of the Commission is no longer necessary. According to van der Spoel's (1976) list of synonyms the last author using the name *C. proboscidea* was Woodward (1880, p. 351) which satisfies art. 23.9.1.1 ICZN. Using the same list of van der Spoel it is clear that in the period 1956–1974 at least 18 authors applied the name *C. peroni* (or *C. peronii*) as valid (satisfying art. 23.9.1.2).

In accordance with art. 23.9.2, considering the names *Cymbulia proboscidea* Lamarck, 1816 and *C. peroni* de Blainville, 1818, the younger name is here considered valid (*nomen protectum*) and the older name as invalid (*nomen oblitum*).

*Cymbulia* sp. 1

Pl. 22, figs. 4–6

Discussion—The minute larval shells are not rare in several samples (but of course absent in samples of which the finer fractions were not available). As Cymbuliidae are predominantly known from the living animals and/or their pseudoconchs, very little informa-

tion on the larval shell is to be found in literature. So much is clear that these larval shells have only one and a half whorl at the most, rapidly increasing in diameter, which distinguishes them from abundantly co-occurring juvenile *Heliconoides inflata* of the same size.

The present specimens are considered to belong to the genus *Cymbulia*, in which two types are distinguished. The most common of them is indicated here *Cymbulia* sp. 1. It is present in 9 of the 15 samples, sometimes with up to 40 specimens. It differs from *Cymbulia* sp. 2 in being larger and by the larger diameter of the nucleus (c. 0.08 mm). H of a complete shell of one whorl is c. 0.50 mm, shell height c. 0.36 mm. Its aperture is large and round. The base clearly umbilicated.

### *Cymbulia* sp. 2

Pl. 22, figs. 7–9

Discussion—Found in four samples (nrs 7, 8, 11 and 13) in just one to three specimens, apart from sample 7, which yielded 19 specimens. They are smaller than *Cymbulia* sp. 1, but have a quarter of a whorl more. The nucleus is only c. 0.04 mm. One of the larger specimens measures H = 0.18 mm, W = 0.30 mm.

Family Peraclididae Tesch, 1913

Genus *Peraclis* Forbes, 1844 (emend. Pelseneer, 1888)

Type species—*Atlanta reticulata* d'Orbigny, 1836 (Recent).

### *Peraclis moluccensis* Tesch, 1903

Pl. 23, fig. 1

1903 *Peraclis moluccensis* n. sp.; Tesch, p. 112.

1976 *Peraclis moluccensis* Tesch, 1903—van der Spoel, p. 31, fig. 12.

Discussion—Just a few damaged or juvenile specimens were found in the Gulf of Aden (sample 15). Van der Spoel's distribution map (1976, fig. 171) does not include the Gulf of Aden, but the northern limit in the Indian Ocean comes quite close to that area. Richter (1979, p. 22) did not find this species in the Indian Ocean, but reported specimens of *Peraclis apicifulva* Meisenheimer, 1906, a species not represented in my samples.

Measurements of the largest specimen: H = 1.72 mm, W = 1.74 mm, number of whorls = 2¾.

### *Peraclis reticulata* (d'Orbigny, 1836)

Pl. 23, figs. 2, 3

1836 *Atlanta reticulata*, d'Orb.; d'Orbigny, p. 178, pl. 12, figs. 32–35, 39.

1976 *Peraclis reticulata* (d'Orbigny, 1836)—van der Spoel, p. 28, fig. 9.

Discussion—Well-preserved specimens of this species

are common in most samples, all over the Red Sea, but absent in samples 1–2 and 14 and with just 8 specimens in the Gulf of Aden sample (nr. 15). In three of the four northwesternmost samples from the Red Sea proper many specimens in internal mould preservation are present. Van der Spoel (1976, fig. 168) excluded the northern Indian Ocean (inclusive of the Red Sea) from the distribution pattern of this species. Almogi-Labin & Reiss (1977, pl. 10, fig. 4), however, recorded this species from plankton hauls, from Holocene bottom sediments and from glacial and interglacial sediments in cores in the Gulf of Aqaba and the northernmost Red Sea. Bandel & Hemleben (1995, p. 227, figs. 1A, B) described larval development of this species based on Red Sea specimens.

*Peraclis reticulata* is easily recognised by its sinistral, relatively high conical shell with convex whorls, on the earliest ones of which frequently the cuticulum with reticulate ornament is preserved (Pl. 23, fig. 3). The aperture is quite large, and the columella is prolonged downward into a rostrum. As the shell wall is very fragile the apertural margin is broken in all specimens, and therefore the more solid rostrum usually seems to be more prominent. On the body whorl there is a faint spiral below the upper suture. On this spiral the initially opisthocyrt growth lines turn to prosoclyne, but the spiral does not develop to a spine on the apertural margin. This species does not demonstrate the radial subsutural crests as seen in other *Peraclis* species.

Measurements of a larger specimen (sample 12): H = 3.42 mm, W = 2.16 mm, number of whorls 3¾. A large specimen in internal mould preservation (sample 3) reaches a height of 3.90 mm. Van der Spoel (1976) indicates a maximum shell height of 6 mm.

### Gymnosomata

Note—The Gymnosomata are a group of in the adult stage shell-less, so-called 'naked' pteropods, presently subdivided in two superfamilies, Clionoidea Rafinesque, 1815 and Hydromyloidea Pruvot-Fol, 1942. In Clionoidea four families are recognised (Clionidae, Cliopsidae, Notobranchaeidae and Pneumodermatidae). In Hydromyloidea are two families, Hydromylidae and Laginiopsidae (Bouchet & Rocroi, 2005, p. 259). Altogether, some 50 species are currently accepted in the Gymnosomata (Lalli & Gilmer, 1989, p. 208).

Knipowitsch (1891) and Lebour (1931) studied the entire life cycle of a common gymnosome species, *Clione limacina* (Phipps, 1774), a coldwater species occurring in both arctic and antarctic areas. Numerous studies on anatomy, feeding and reproduction were published (for references see Lalli & Gilmer, 1989, p. 209). *C. limacina* also was the subject of a large number of neurophysiological studies in the 19-eighties and -nineties (for references see <http://www.biol.sc.edu/~vogt/courses/neuro/neurobehavior.html#clione>).



Of several gymnosome species it is known that the veliger larvae possess a shell, which is shed at the beginning of metamorphosis. Lalli & Conover (1973, 1976) studied and illustrated embryonic shells of three species, viz. *Clione limacina*, *Paedoclione doliiformis* Danforth, 1907 and *Pneumoderma atlanticum* (Oken, 1815).

Possibly most, if not all gymnosomatous species have a shell in their veliger stage, but of all the other species this shell is still unknown. Lalli & Conover (1976, p. 239) wrote 'it may be that some gymnosome species have a reduced larval shell, or none at all in free-swimming stages.' Also they state (p. 237) that 'gymnosome shells can be collected in plankton tows or bottom samples, but they often go unrecognized by planktologists and geologists.' For further discussion on gymnosomatous larval shells and their misidentification as protoconchs of the euthecosomatous pteropod *Clio polita* (Pelseneer, 1888) see Janssen (in press).

Van der Spoel & Diester-Haass (1976) also published finds of unidentified gymnosomatous larval shells, from plankton samples, as well as from ocean bottom cores off NW Africa and Portugal, sampled just below the Holocene/Pleistocene boundary. Their drawing of a fossil specimen resembles the larval shell of *Paedoclione*, as given by Lalli & Conover (1976), with which they indeed compare their specimens (misspelling the name, by the way, as *P. doliiformis*!). They concluded that they were not identical, considering differences in measurements and distribution.

In the present study four different types of gymnosomatous larval shells were found, and one of these quite abundantly. As they all basically resemble the *Paedoclione*-type they are supposed to represent species of the Clionidae family. In addition, three further gymnosomatous larval shell types from the Red Sea were recorded by Kunz (1996). They are discussed below.

Superfamily Clionoidea Rafinesque, 1815 ?

Family Clionidae Rafinesque, 1815 ?

#### Gymnosomata sp. 1

Pl. 23, figs. 4–7; Pl. 24, fig. 1

(1996) Gymnosomata Typ I—Kunz, p. 170, pl. 32, fig. 1 (non fig. 2).

Discussion — Specimens of this type are quite common in several samples (nrs 7, 11 and 13), rare in others (nrs 9, 12, 14 and 15) and absent in the remaining samples. Similar specimens were illustrated by Almogi-Labin & Reiss (1977, pl. 2, fig. 1) from the Gulf of Eilat and by Kunz (1996, pl. 32, fig. 1) from the Red Sea and the western Arabian Sea, respectively.

The shell consists of three parts. Total shell height reaches c. 270 µm in the largest specimens. The initial shell part (protoconch-1) is spherical and smooth (H = 140–190 µm, W = 160–200 µm), dorso-ventral di-

ameter slightly less than the shell width. After a strong constriction, in which short vertical ridges are seen, follows a further shell part (protoconch-2), shaped as an apertural collar. This collar is slightly swollen and has a smooth surface. Its central parts are slightly more produced abapically than the sides. After a sharp boundary and a slight constriction follows a third shell part clearly demonstrating growth lines (early teleoconch?). Slightly irregular longitudinal ridges are present on this latter part of the shell (magnification  $\times 300$ ). In a lateral view (Pl. 23, fig. 7a) it is seen that the apertural margins are slightly bent together dorso-ventrally, resulting in an elliptical aperture. The shell part with growth lines sometimes is absent (Pl. 23, fig. 6, the specimen presumably died premature, before hatching or metamorphosis), or can be more or less strongly developed (Pl. 23, figs. 4a, 5a).

Closely resembling my specimens is what Kunz (1996) illustrated in his pl. 32, fig. 1, from the western Arabian Sea. That specimen differs solely by smaller dimensions and a higher and slightly more oval initial shell part. Its height reaches almost 200 µm, and shell width is 128 µm.

#### Gymnosomata sp. 2

Pl. 24, fig. 2

Discussion—Just a single incomplete specimen was found in sample 7. It has a preserved shell height of 200 µm and differs from the foregoing form by its relatively higher elliptical protoconch-1 shape.

#### Gymnosomata sp. 3

Pl. 24, fig. 3

Discussion—Of this form just two specimens were encountered in sample 7. It differs clearly and in several respects from Gymnosomata sp. 1. Its shell height reaches 262 µm, but the spherical initial part is small, with a height of c. 150 µm, and relatively higher. The constriction between protoconch-1 and the younger part of the shell is distinct. A separation between protoconch-2 and a possible early teleoconch is not clear: growth lines seem to develop immediately after the constriction. The upper half of protoconch-1 demonstrates spaced radial ridges, continuing on the lower half of the younger part of the shell, but interrupted in the constriction. At stronger magnification these ridges seem to be built up from close-set granules. A much finer and more irregular radial striation is present on the upper half of the shell part above the constriction.

#### Gymnosomata sp. 4

Pl. 24, fig. 4a, b

Discussion—Two specimens were found, in samples 7 and 13 one each. They agree with the general gymnosomatous shell type by being composed of

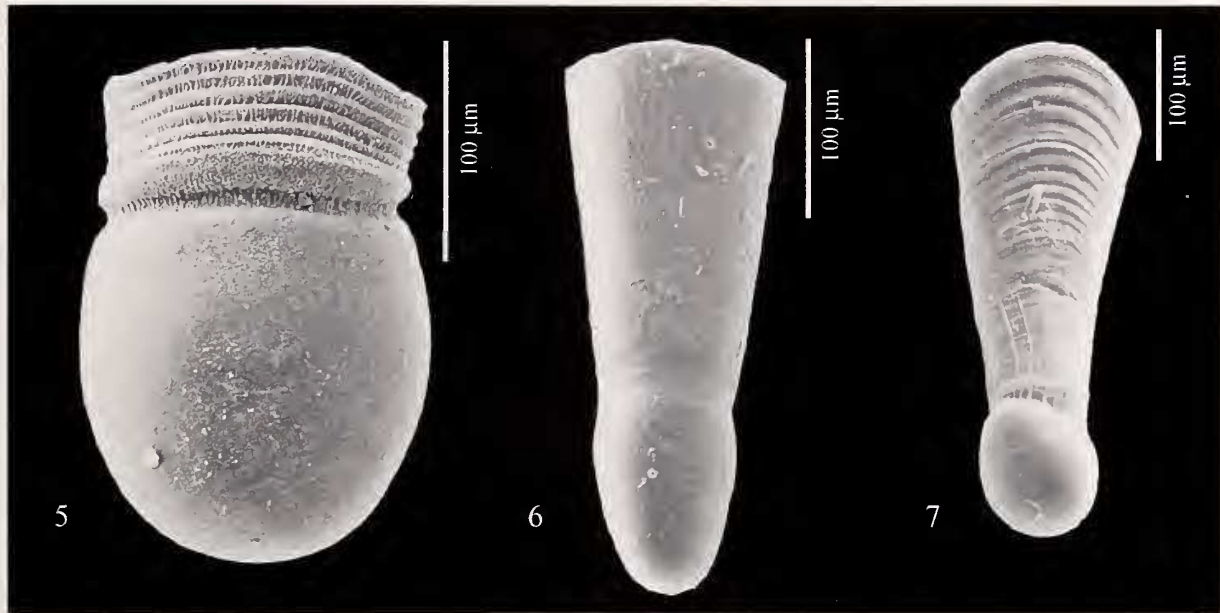


Figure 5–7. Gymnosomatous larval shells from the Red Sea (after Kunz, 1996, pl. 32, figs. 2–4). 5: *Gymnosomata* Typ I *sensu* Kunz (1996); 6: *Gymnosomata* Typ IIa *sensu* Kunz (1996); 7: *Gymnosomata* Typ IIb *sensu* Kunz (1996).

a spherical initial shell part and a cylindrical protoconch-2/teleoconch part, but the differences are obvious. The smooth protoconch-1 is small (height = 143 µm) and more elongately elliptical (width = 105 µm). The constriction between protoconchs-1 and -2 is weak and protoconch-2 is very slightly swollen. The upper boundary of this shell part (indicated by > on Pl. 24, fig. 4a) is distinct by the start of very fine longitudinal ridges (Pl. 24, fig. 4b) and growth lines. This early teleoconch part of the shell widens slightly and its surface shows irregular undulation.

Note—Kunz (1996) illustrated three further gymnosomatous shells from the Red Sea (reproduced here in Text-figs. 5–7) that also have a further shell part beyond protoconch-1, but differ in details.

The specimen illustrated by Kunz (1996, pl. 32, fig. 2) resembles *Gymnosomata* sp. 1, but its third shell part shows regular transverse ribbing and more densely distributed longitudinal striation. It reaches 235 µm shell height. Presumably it does not belong to the same species. In Table 2 I indicate this form as *Gymnosomata* Typ I *sensu* Kunz (1996). His illustration is copied here as Text-fig. 5.

*Gymnosomata* Typ IIa (Kunz, pl. 32, fig. 3) has an oval, slightly pointed protoconch-1, a vague constriction, and a protoconch-2 that is only separated from the early teleoconch by the start of longitudinal ornament (Text-fig. 6).

*Gymnosomata* Typ IIb (Kunz, 1996, pl. 32, fig. 4) has a spherical protoconch-1, a clear constriction, behind

which a protoconch-2 is not very distinct. Immediately after the constriction relatively coarse and distant radial ridges develop on the early 1/3rd part of the teleoconch, which moreover is distinctly annulated (Text-fig. 7).

#### Superfamily *incertae sedis*

#### Veliger larva of unknown gastropod species?

##### Pl. 24, figs. 5–7

Discussion—Material of the present species is common to abundant in various samples, but is absent in samples 1–2, 4–6, 10 and 12. Bandel et al. (1997) did not record this mollusc type in their plankton hauls from the Red Sea, but Professor Klaus Bandel (in litt., 2006) told me that he did catch them indeed. At the time he suspected them to be larvae of the nudibranch *Glaucus*, but this can't be acknowledged, as the adult specimens did not reproduce and therefore their larval shell and metamorphosis could not be studied. So, these specimens still remain unidentified. In a paper by Bebbington (1986) larvae of *Glaucus atlanticus* Forster, 1777 are described, and an early shell is illustrated (Bebbington, fig. 8e), but this drawing can't be related to the present specimens.

The sinistral shells are very small ( $H = c. 250 \mu\text{m}$ ,  $W = c. 200 \mu\text{m}$ ) and fragile. Their overall shape is ovoid, the number of whorls is barely more than two. The apertural margin is provided with two deep circular incisions, one just below the suture, the other near the base of the shell. The incisions have a thickened margin



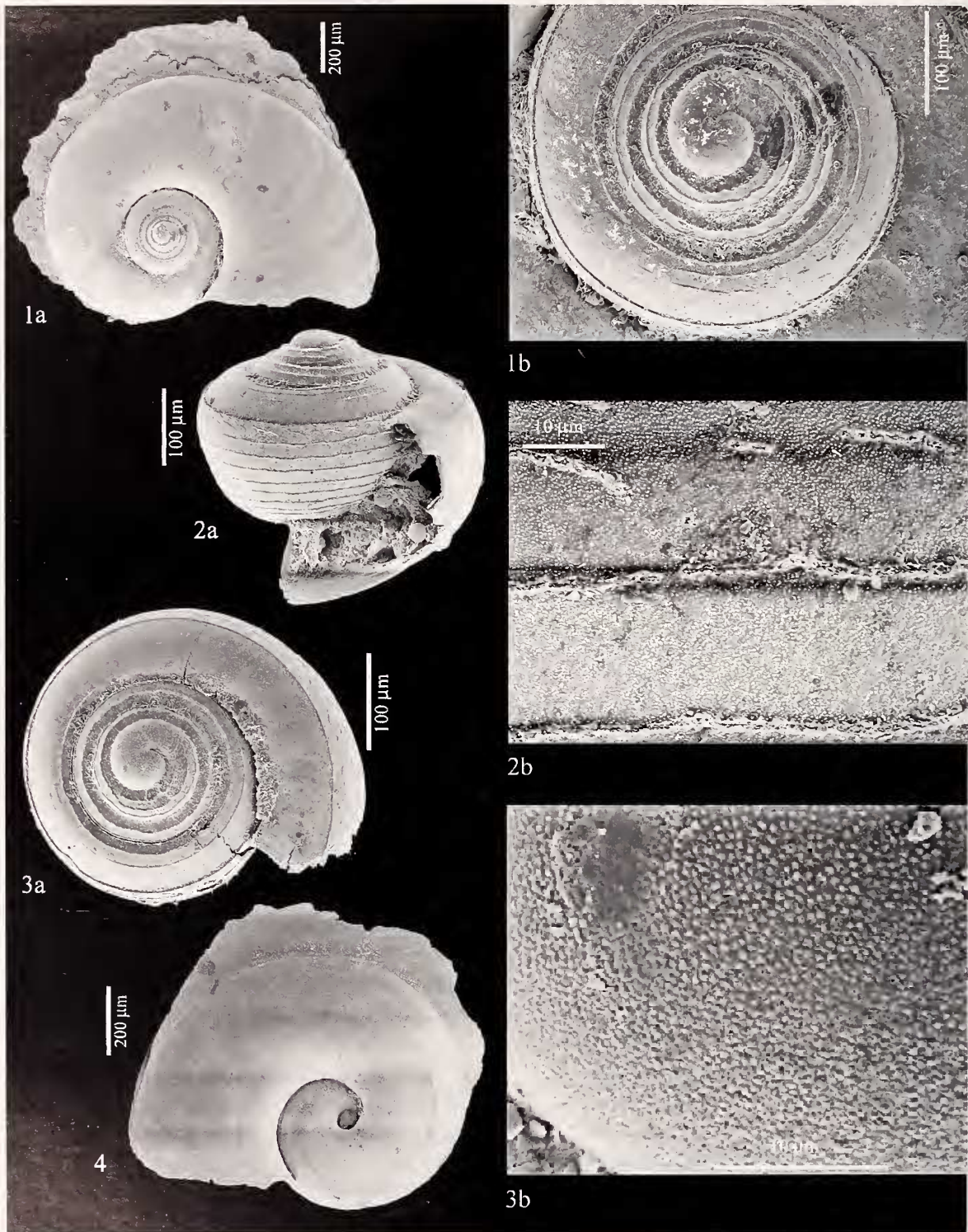


Plate 1. SEM-images of *Atlanta echinogyra* Richter, 1972 (Figures 1–4, Red Sea, sample 11, RGM 540.347–540.350). Figure 1a: adult specimen, apical view; Figure 1b: protoconch enlarged; Figure 2a: protoconch, oblique apertural/apical view; Figure 2b: micro-ornament just below the shoulder spiral; Figure 3a: protoconch, apical view; Figure 3b: micro-ornament of nucleus; Figure 4: adult specimen, umbilical view.

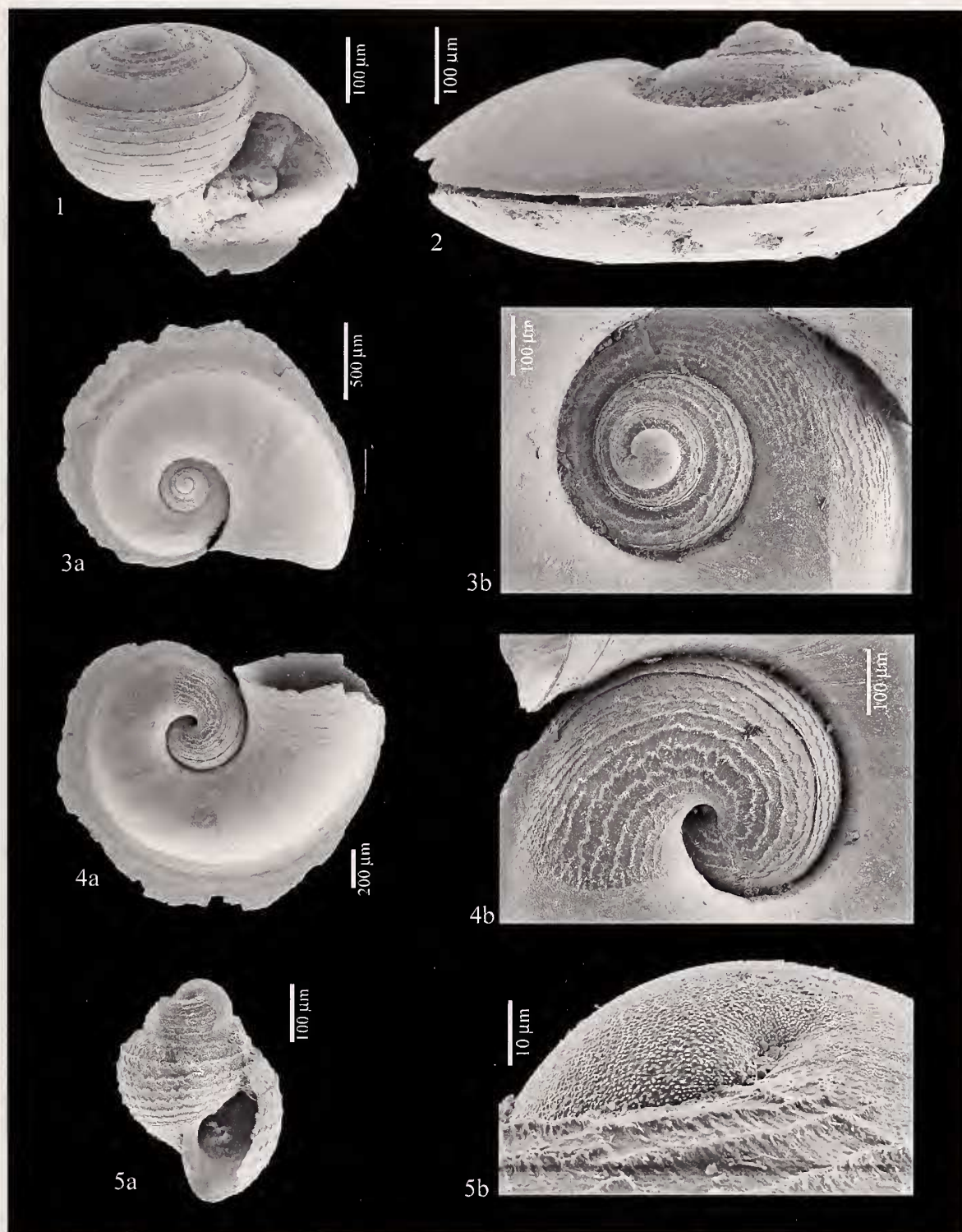


Plate 2. SEM-images of *Atlanta echinogyra* Richter, 1972 (Figures 1–2; Red Sea, sample 11, RGM 540.351–540.352) and *A. fusca* Souleyet, 1852 (Figures 3–5, Red Sea, sample 12, RGM 540.353–540.354; sample 13, RGM 540.355). Figure 1: protoconch, oblique apertural/apical view; Figure 2: adult specimen, posterior view; Figure 3a: adult specimen, apical view; Figure 3b: protoconch enlarged; Figure 4a: adult specimen, umbilical view; Figure 4b: protoconch enlarged, umbilical view; Figure 5a: protoconch, apertural view; Figure 5b: micro-ornament of nucleus.



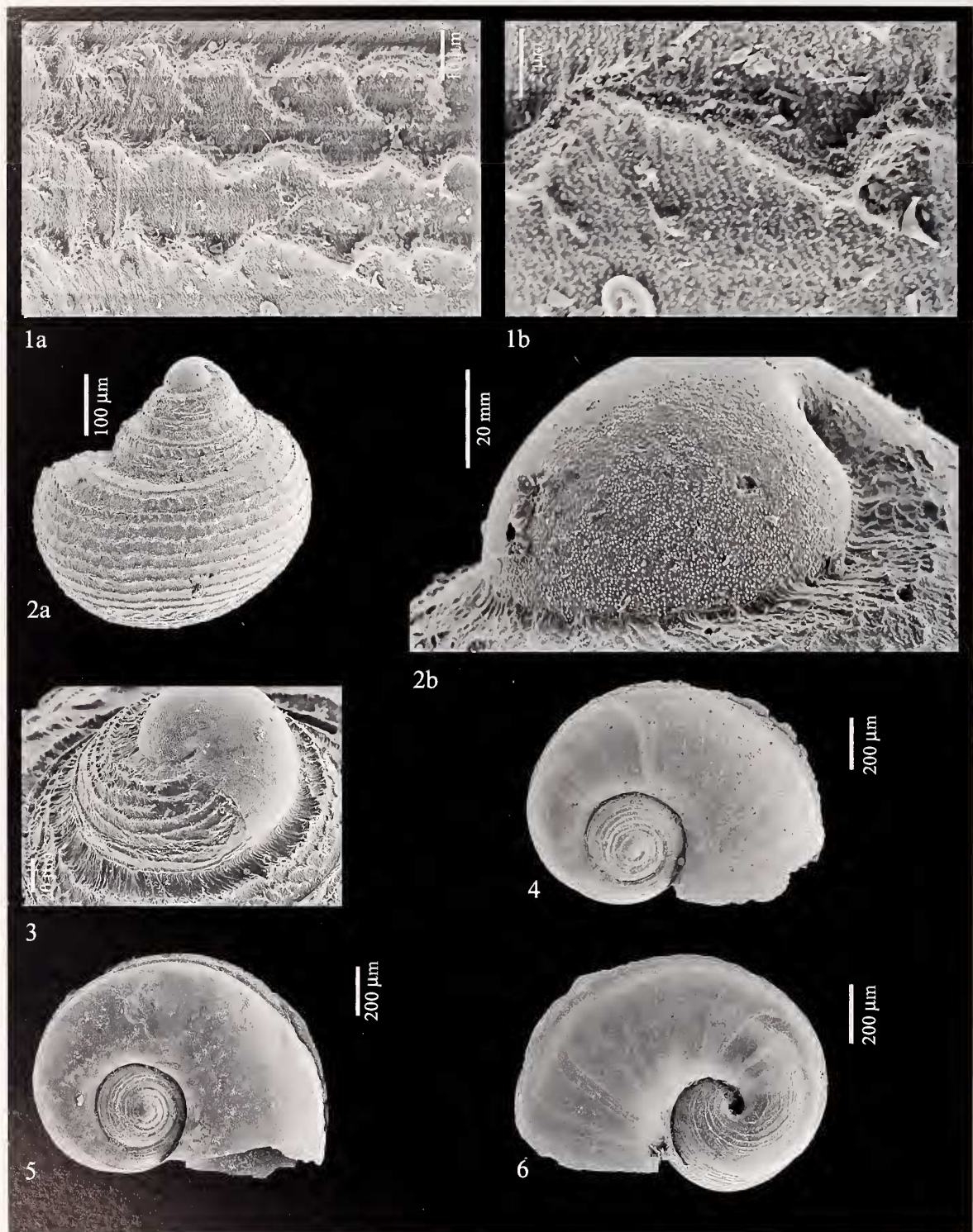


Plate 3. SEM-images of *Atlanta fusca* Souleyet, 1852 (Figures 1–3, Red Sea, sample 13, RGM 540.355–540.357) and *Atlanta helicinoides* Souleyet, 1852 (Figures 4–6, Red Sea, sample 13, RGM 540.358–540.360). Figure 1a: spirals in zigzag-shape of protoconch illustrated Pl. 2, fig. 5; Figure 1b: same, more strongly enlarged; Figure 2a: protoconch, posterior view; Figure 2b: micro-ornament of nucleus; Figure 3: nucleus and early whorl of protoconch; Figures 4, 5: adult specimens, apical views; Figure 6: adult specimen, umbilical view.



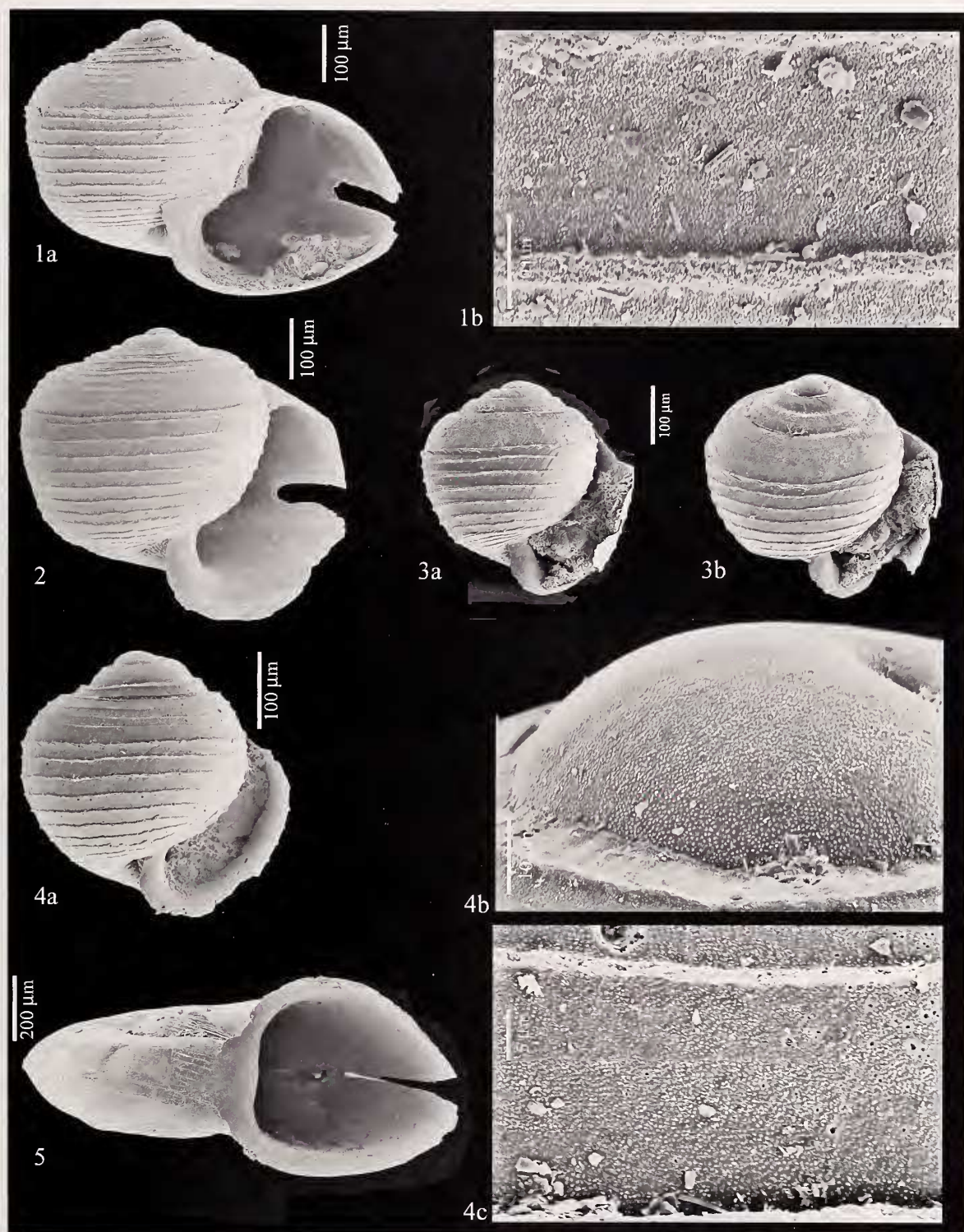


Plate 4. SEM-images of *Atlanta helicinoides* Souleyet, 1852 (Figures 1–5, Red Sea, sample 13, RGM 540.361–54.364; sample 11, RGM 540.365). Figure 1a: protoconch, apertural view; Figure 1b: micro-ornament between peripheral spirals; Figure 2: protoconch, apertural view; Figure 3a: protoconch, apertural view; Figure 3b: protoconch, oblique apertural/apical view; Figure 4a: protoconch, apertural view; Figure 4b: micro-ornament of nucleus; Figure 4c: micro-ornament between peripheral spirals; Figure 5: adult specimen, apertural view.

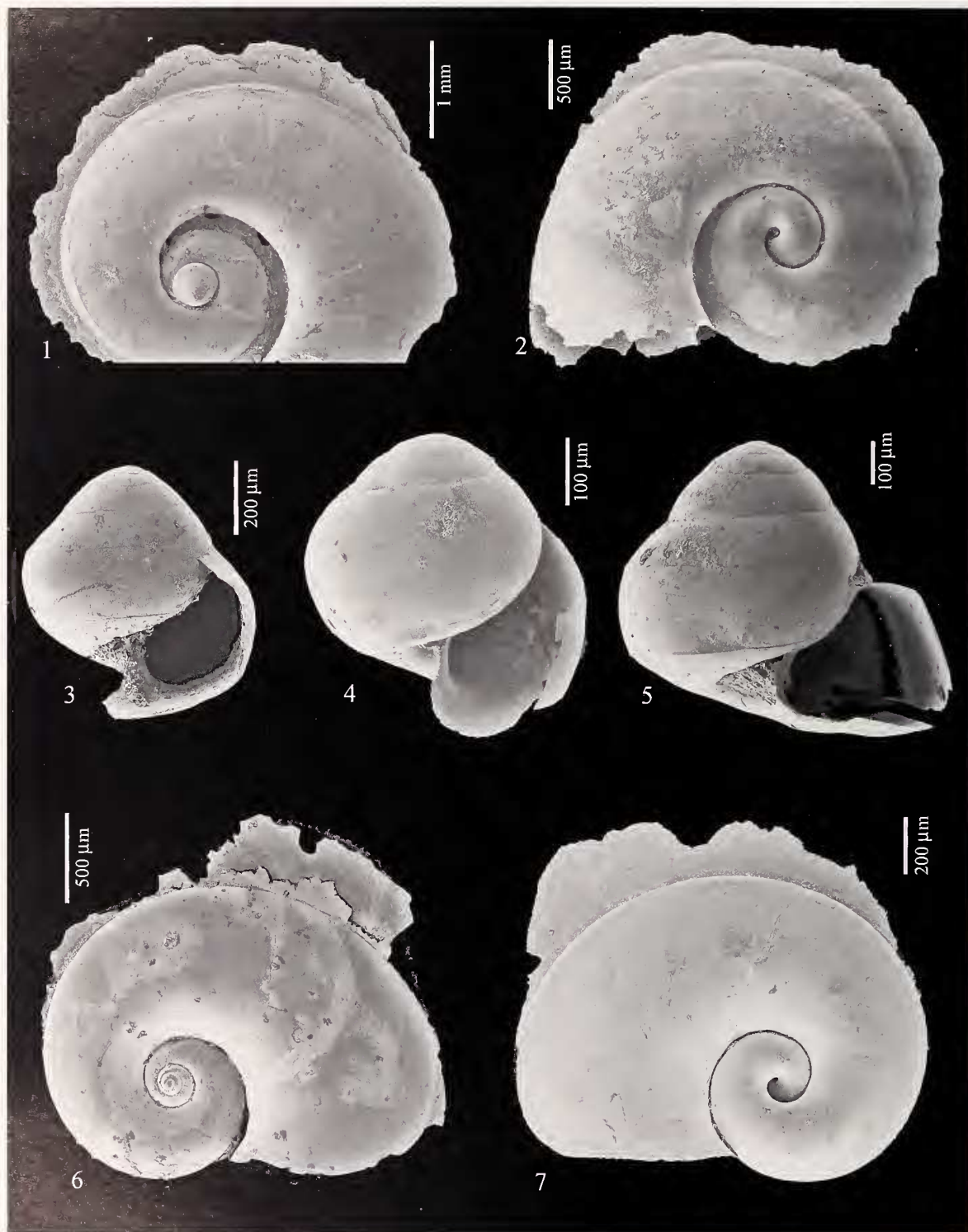


Plate 5. SEM-images of *Atlanta inclinata* Souleyet, 1852 (Figures 1–5, Red Sea, sample 13, RGM 540.366–540.370) and *A. lesueuri* Souleyet, 1852 (Figures 6, 7, Red Sea, sample 13, RGM 540.371–540.372). Figure 1: adult specimen, apical view; Figure 2: adult specimen, umbilical view; Figures 3–5: protoconchs, apertural views; Figure 6: adult specimen, apical view; Figure 7: adult specimen, umbilical view.



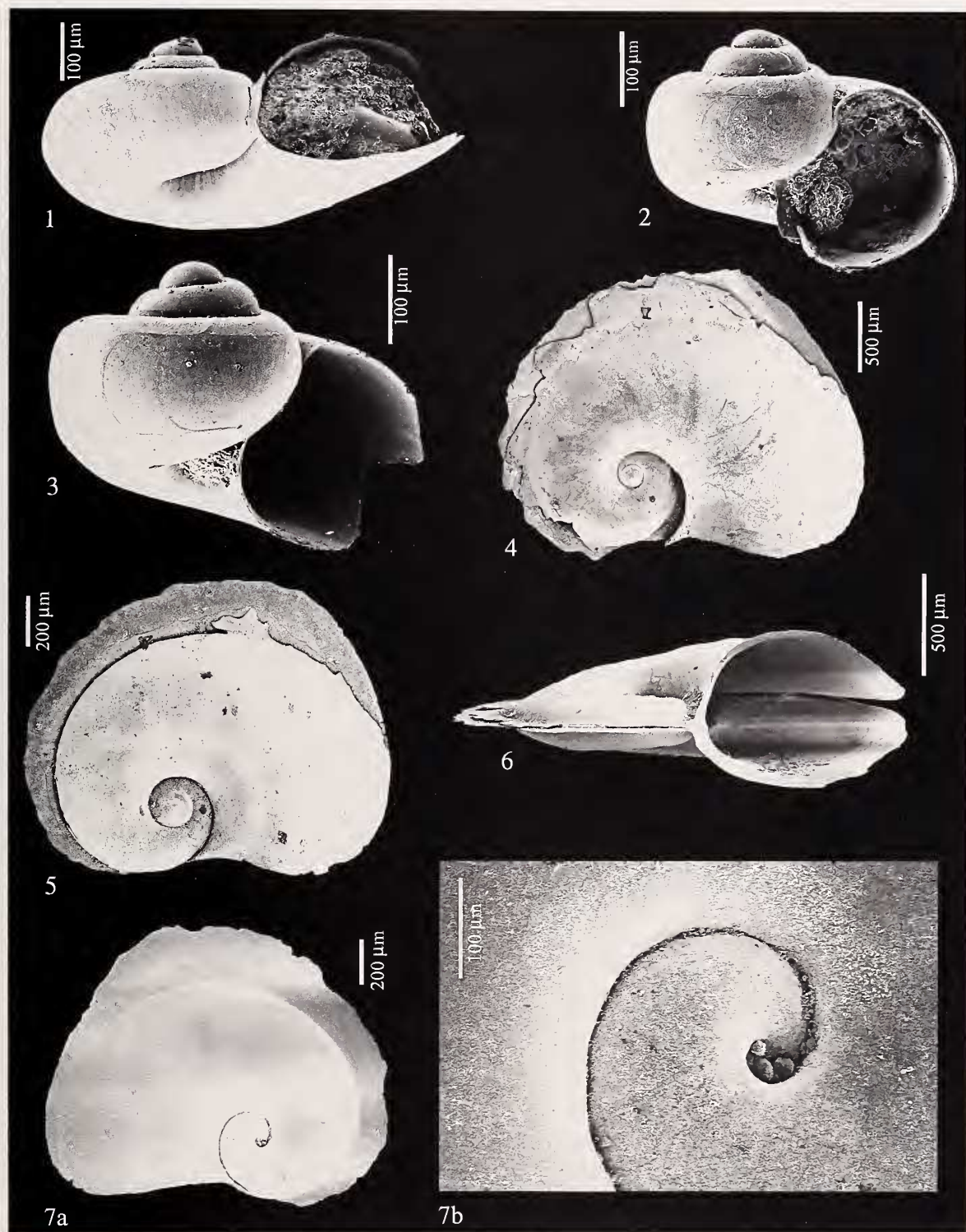


Plate 6. SEM-images of *Atlanta lesueuri* Souleyet, 1852 (Figures 1–3, Red Sea, sample 13, RGM 540.373–540.375) and *A. oligogyra* Tesch, 1906 (Figure 4, Red Sea, sample 6, RGM 540.376; Figures 5 and 7, Red Sea, sample 11, RGM 540.377–540.378, Figure 6, Red Sea, sample 7, RGM 540.379). Figure 1: juvenile specimen, apertural view; Figs. 2, 3: protoconchs, apertural views; Figures 4–6: adult specimens, apical views; Figure 7a: adult specimen, umbilical view; Figure 7b: umbilicus, enlargement of Figure 7a.

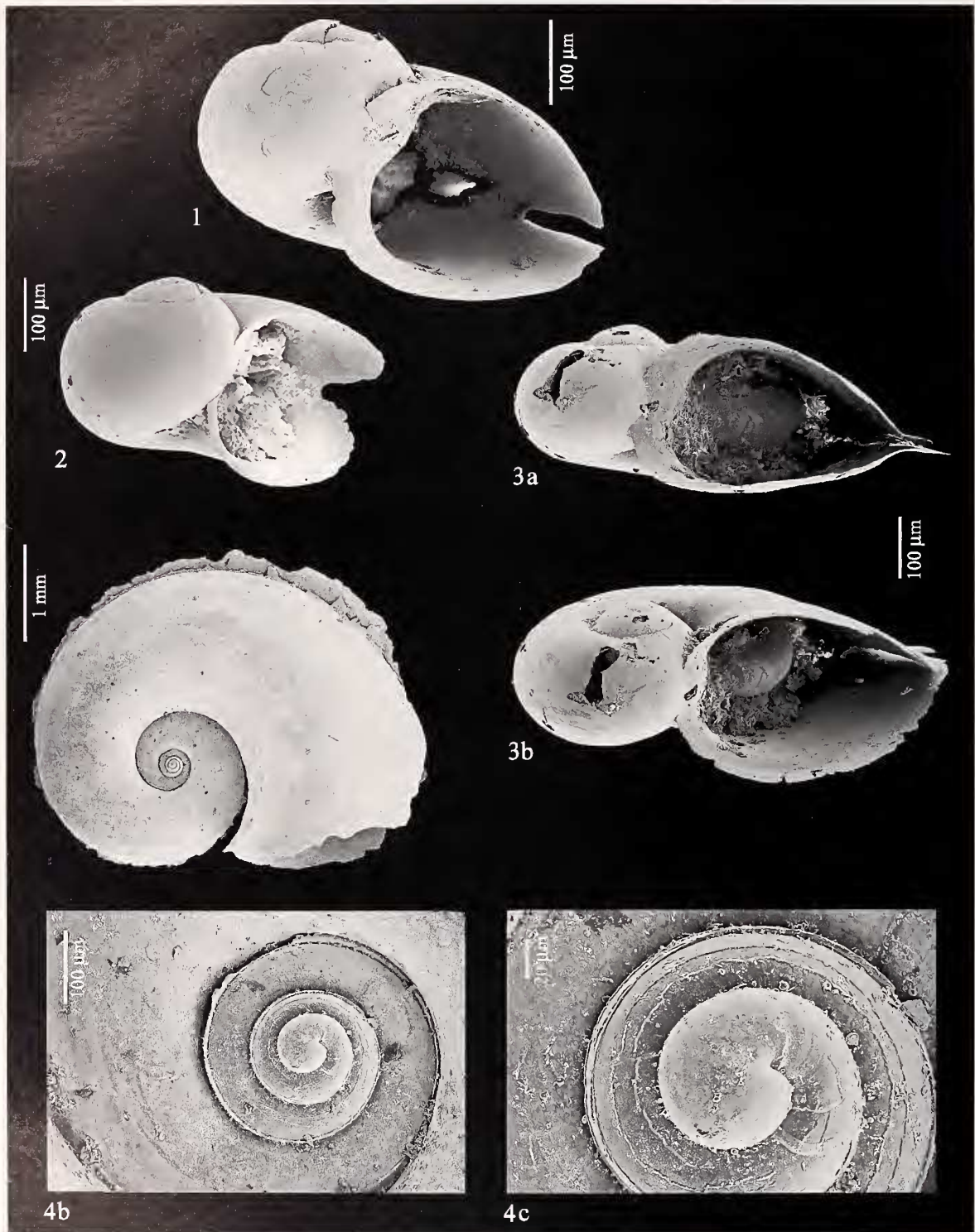


Plate 7. SEM-images of *Atlanta oligogyra* Tesch, 1906 (Figures 1–3, Red Sea, sample 11, RGM 540.380–540.382) and *A. plana* Richter, 1972 (Figure 4, Red Sea, sample 9, RGM 540.383). Figures 1–2: protoconchs, apertural views; Figure 3a: semi-adult specimen, apertural view; Figure 3b: idem, oblique apertural/apical view; Figure 4a: adult specimen, apical view; Figure 4b: idem, protoconch enlarged; Figure 4c: idem, nucleus and first whorl enlarged.



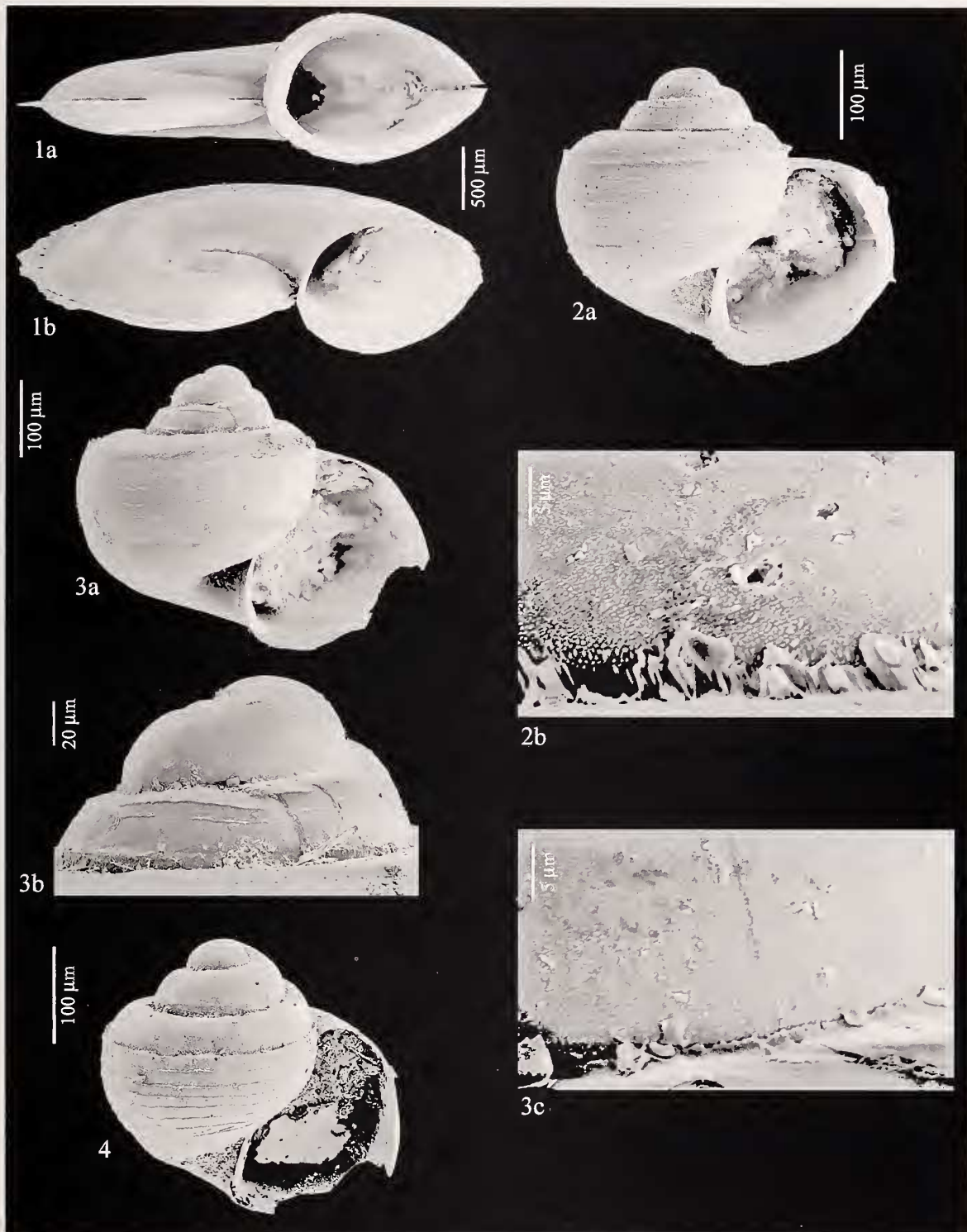


Plate 8. SEM-images of *Atlanta plana* Richter, 1972 (Figure 1, Red Sea, sample 11, RGM 540.384; Figures 2–4, Red Sea, sample 13, RGM 540.385–540.387). Figure 1a: adult specimen, apertural view; Figure 1b: idem, oblique apertural/apical view; Figure 2a: protoconch, apertural view; Figure 2b: micro-ornament of nucleus; Figure 3a: protoconch, apertural view; Figure 3b: micro-ornament of nucleus; Figure 4: protoconch, apertural view.



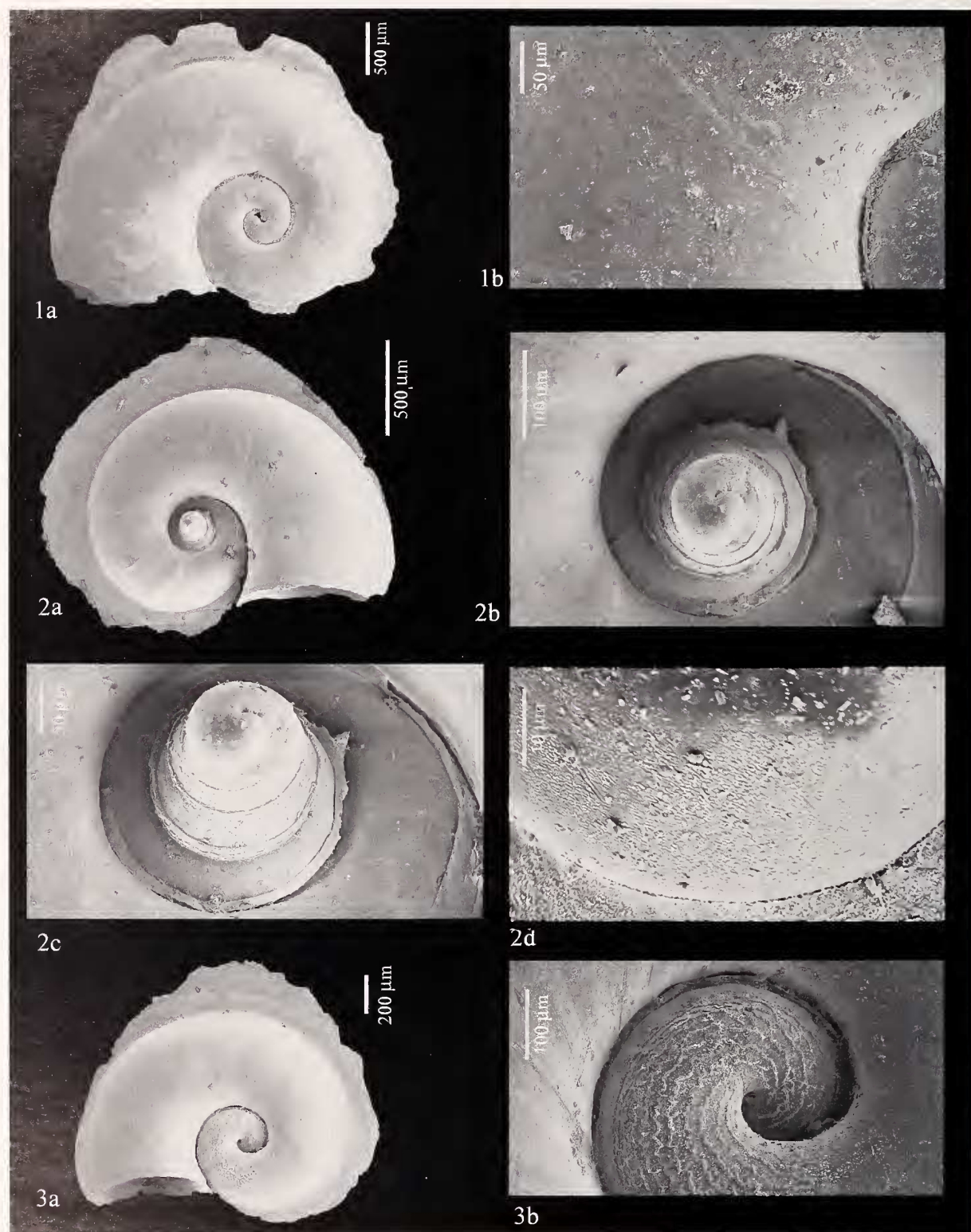


Plate 9. SEM-images of *Atlanta plana* Richter, 1972 (Figure 1, Red Sea, sample 13, RGM 540.388) and *A. turriculata* d'Orbigny, 1836 (Figures 2–3, Red Sea, sample 12, RGM 540.389–540.390). Figure 1a: adult specimen, umbilical view; Figure 1b: enlargement of Figure 1a; Figure 2a: adult specimen, apical view; Figure 2b: protoconch of same specimen; Figure 2c: oblique view of same; Figure 2d: micro-ornament of nucleus; Figure 3a: adult specimen, umbilical view; Figure 3b: enlargement of umbilical part of same specimen.

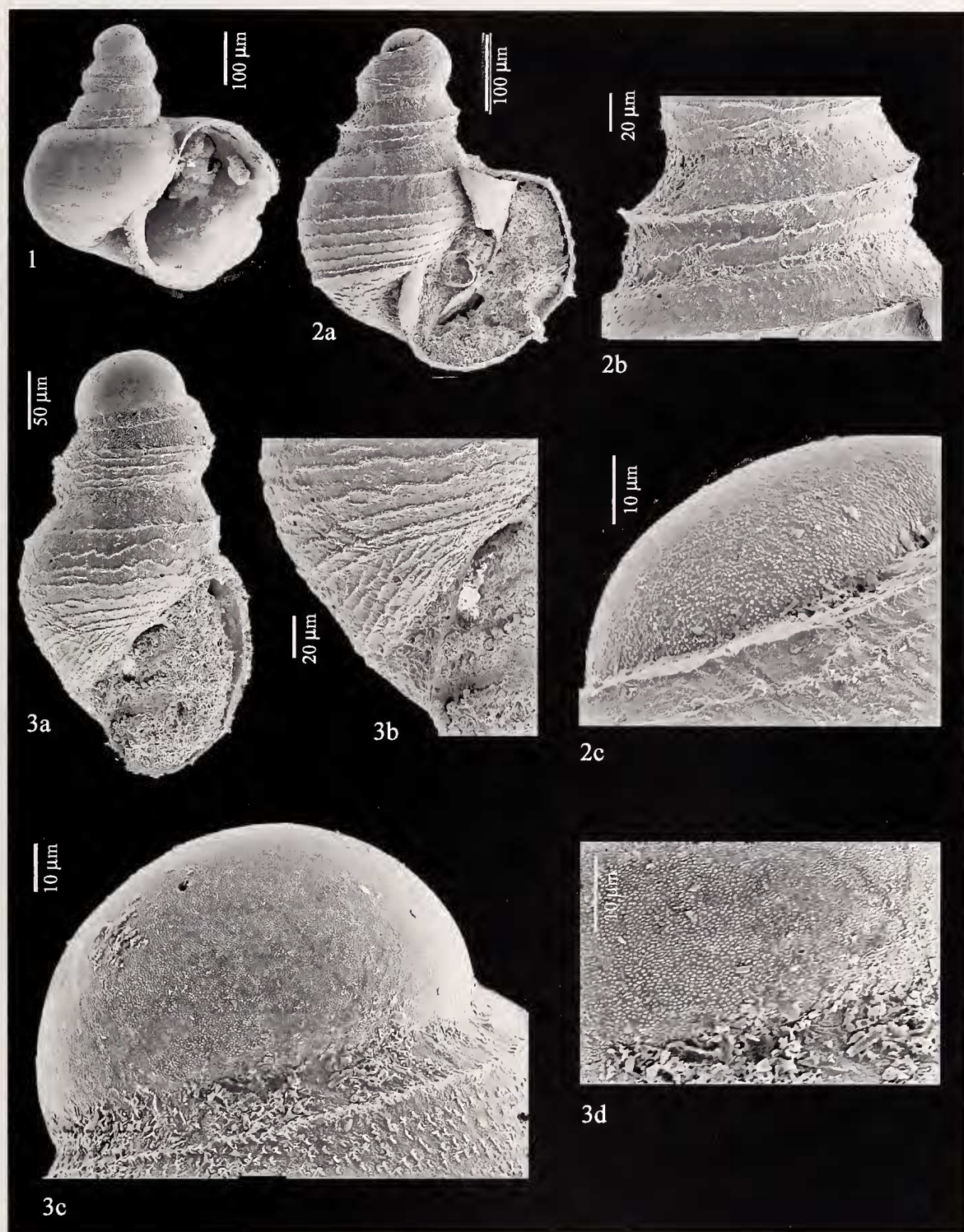


Plate 10. SEM-images of *Atlanta turriculata* d'Orbigny, 1836 (Figures 1, 2, Gulf of Aden, sample 15, RGM 540.391–540.392; Figure 3, Red Sea, sample 13, RGM 540.393). Figure 1: protoconch, apertural view; Figure 2a: protoconch, apertural view; Figure 2b: early whorl of same specimen; Figure 2c: micro-ornament of nucleus of same specimen; Figure 3a: protoconch, apertural view; Figure 3b: ornament on base of same specimen; Figure 3c: nucleus of same specimen; Figure 3d: micro-ornament of nucleus.



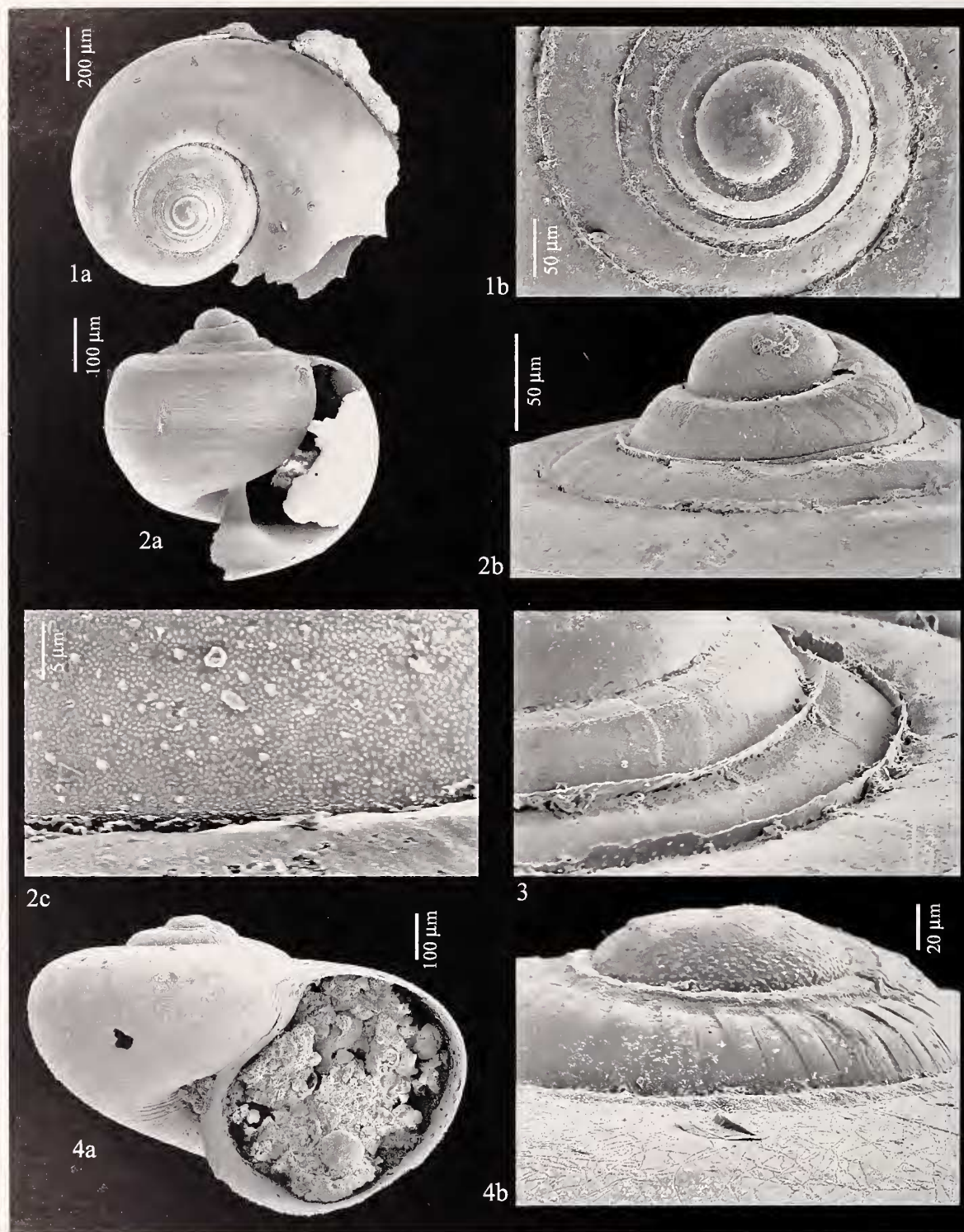


Plate 11. SEM-images of *Atlanta frontieri* Richter, 1993. (Figure 1, Red Sea, sample 11, RGM 540.394; Figures 2, 3, Gulf of Aden, sample 15, RGM 540.395–540.396) and *Carinariidae* sp. 1 (Figure 4, Gulf of Aden, sample 15, RGM 540.397). Figure 1a: juvenile specimen, apical view; Figure 1b: protoconch of same specimen, enlarged; Figure 2a: juvenile specimen, apertural view; Figure 2b: protoconch of same specimen, enlarged; Figure 2c: micro-ornament of nucleus of same specimen; Figure 3: ornament of early whorls; Figure 4a: protoconch, apertural view; Figure 4b: nucleus and first whorl of same specimen, enlarged.

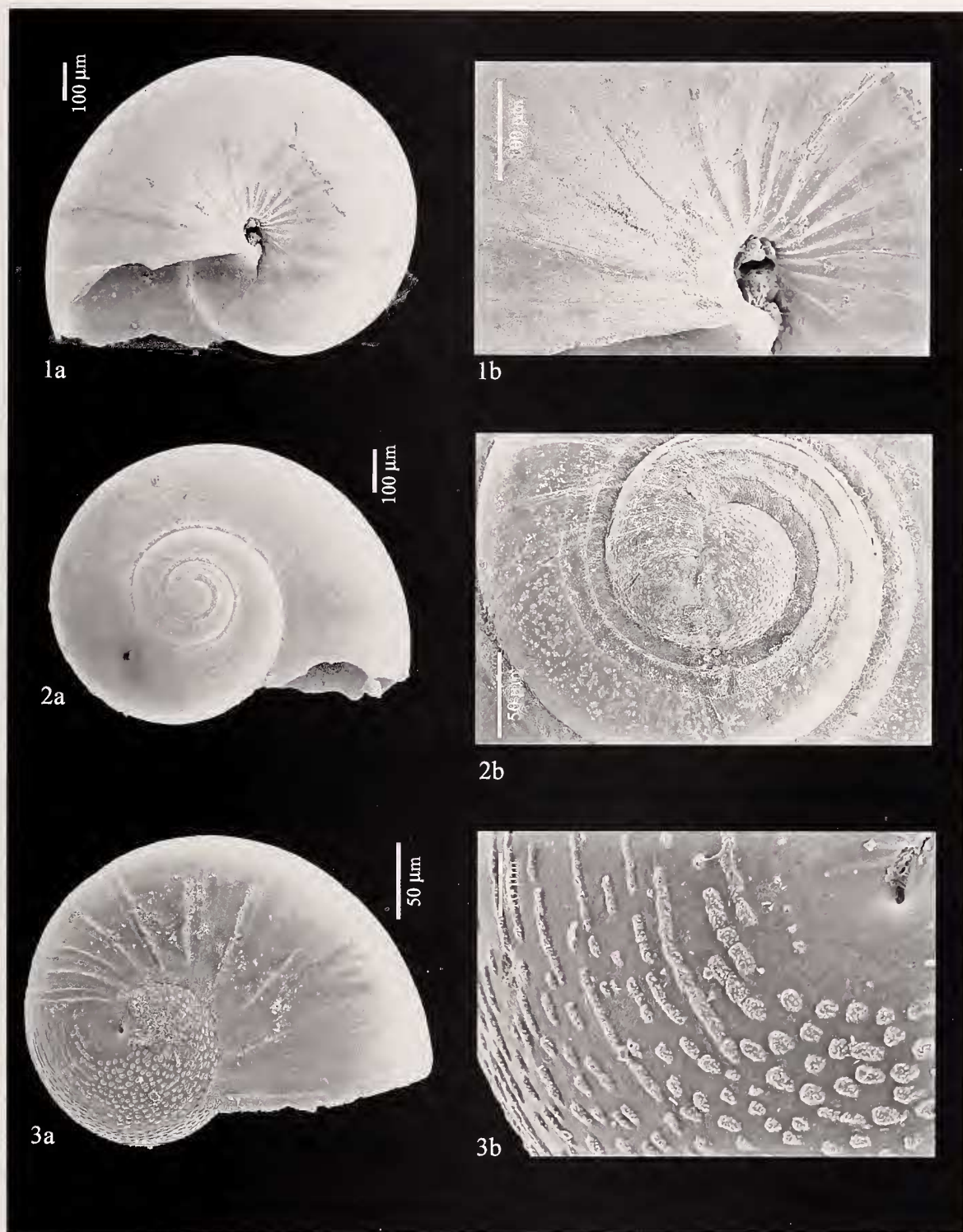


Plate 12. SEM-images of Carinariidae sp. 1 (Figures 1, 2, Gulf of Aden, sample 15, RGM 540.398–540.399) and Carinariidae sp. 2 (Figure 3, Gulf of Aden, sample 15, RGM 540.400). Figure 1a, protoconch, umbilical view; Figure 1b: umbilicus and base of same specimen, enlarged; Figure 2a: protoconch, apical view; Figure 2b: nucleus and first whorl of same specimen, enlarged; Figure 3a: protoconch, apical view; Figure 3b: micro-ornament of nucleus of same specimen.



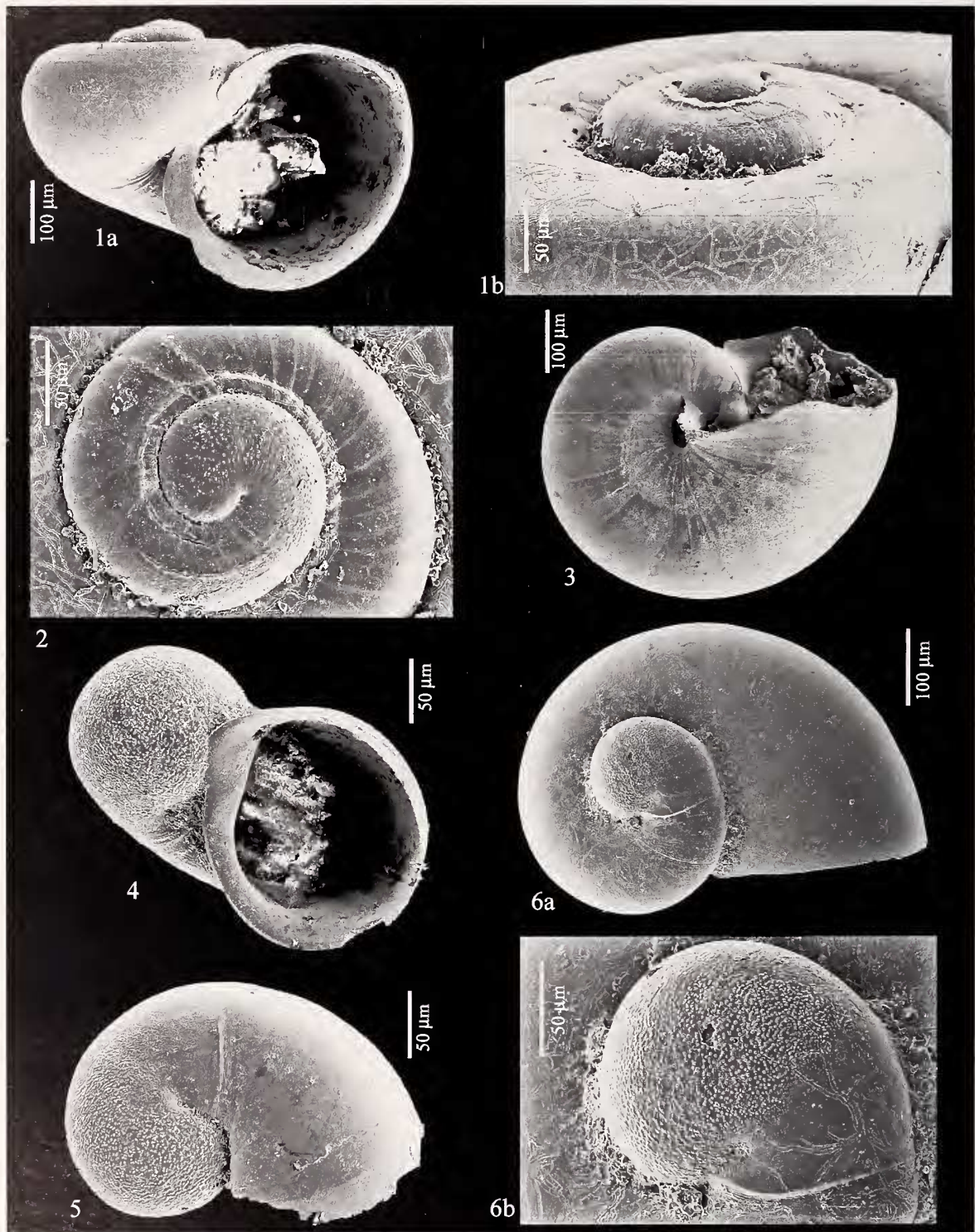


Plate 13. SEM-images of *Carinariidae* sp. 3 (Figures 1–3, Gulf of Aden, sample 15, RGM 540.401–540.403 and *Firoloida demarestia* Lesueur, 1817 (Figures 4–6, Red Sea, sample 7, RGM 540.404–540.405; sample 11, RGM 540.406). Figure 1a: protoconch, apertural view; Figure 1b: oblique apical view of same specimen; Figure 2: nucleus and first whorl, showing micro-ornament; Figure 3: protoconch, umbilical view; Figure 4: nucleus showing micro-ornament, and first half whorl, apertural view; Figure 5: nucleus showing micro-ornament, and first half whorl, apical view; Figure 6a: protoconch, apical view; Figure 6b: nucleus of same specimen, showing micro-ornament.

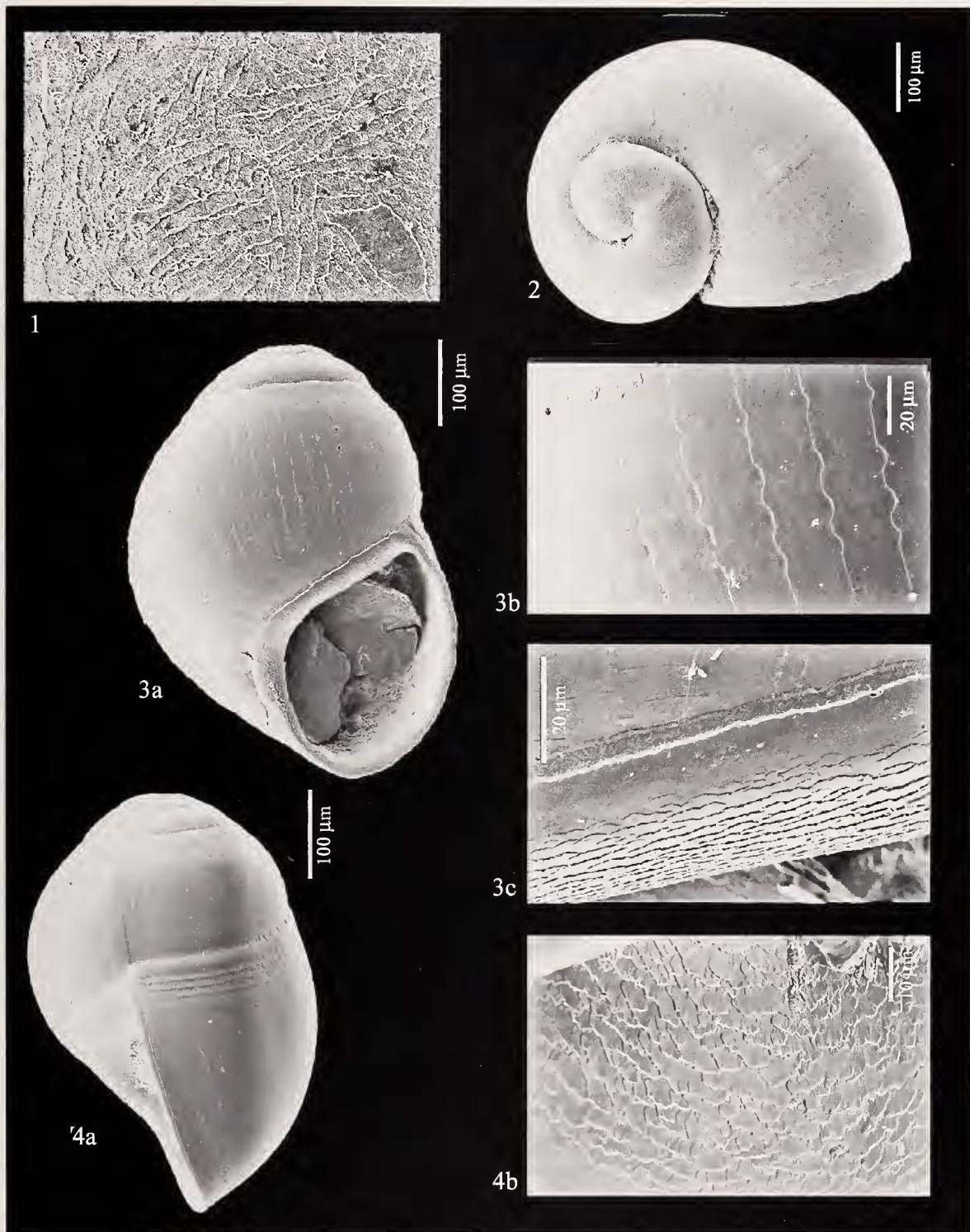


Plate 14. SEM-images of *Fioloida demarestia* Lesueur, 1817 (Figure 1, 2, Red Sea, sample 11, RGM 540.406–540.407) and *Janthina* sp. (Figures 3–4, Red Sea, sample 11, RGM 540.408–540.409). Figure 1: bio-erosion (?) on surface of protoconch illustrated Pl. 13, fig. 6; Figure 2: protoconch, apical view; Figure 3a: protoconch, apertural view; Figure 3b: radial ornament on bodywhorl of same specimen; Figure 3c: aragonite scales on palatal part of apertural margin of same specimen; Figure 4a: protoconch, lateral view; Figure 4b: aragonite scales on columellar callus of same specimen.



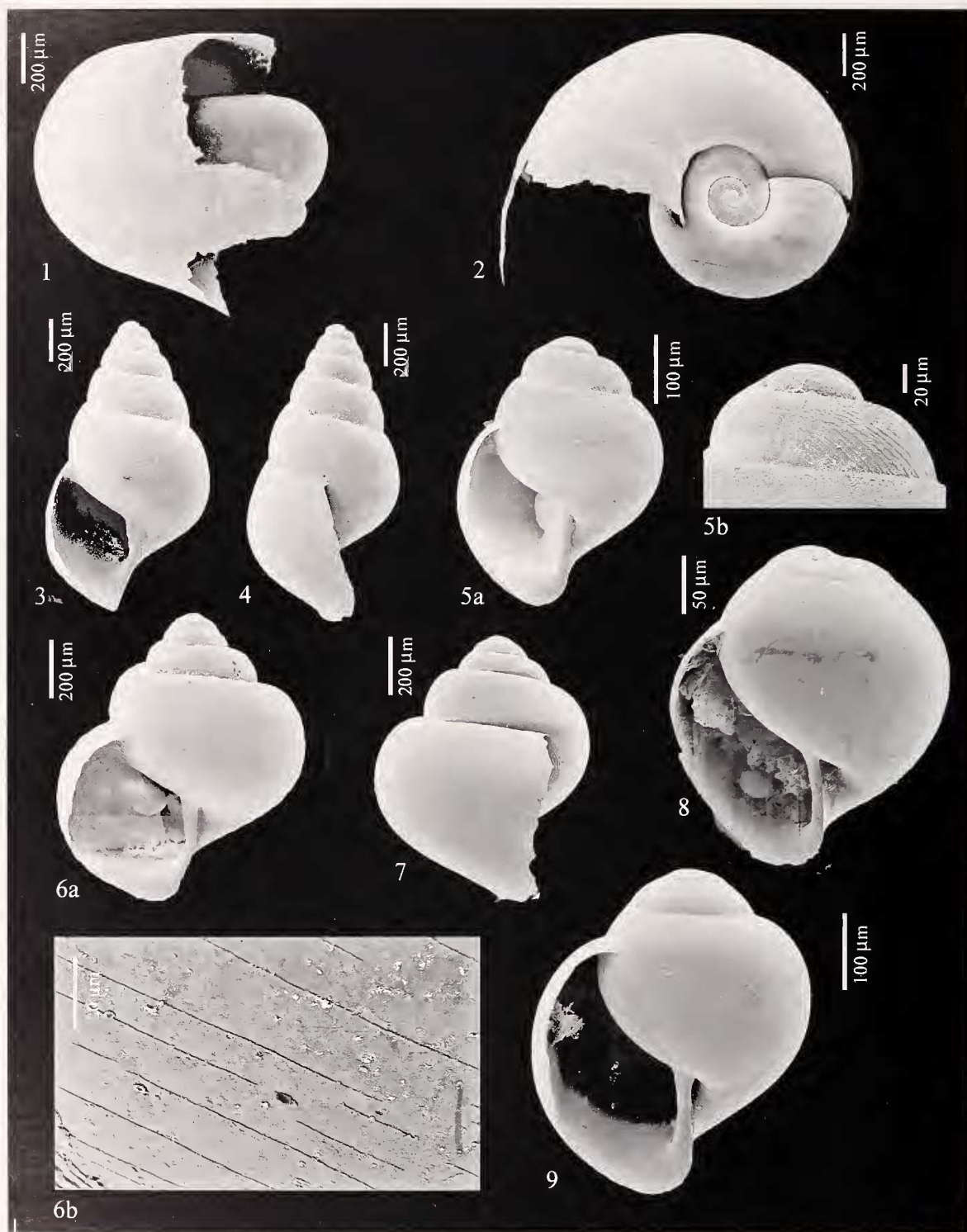


Plate 15. SEM-images of *Heliconoides inflata* (d'Orbigny, 1836) (Figures 1, 2, Red Sea, sample 12, RGM 540.410–540.411); *Limacina bulimoides* (d'Orbigny, 1836) (Figures 3–5, Red Sea, sample 7, RGM 540.412–540.413; sample 13, RGM 540.414) and *Limacina trochiformis* (d'Orbigny, 1836) (Figures 6–9, Red Sea, sample 4, RGM 540.415–540.416; sample 8, RGM 540.417; sample 14, RGM 540.418). Figure 1: adult specimen, lateral view; Figure 2: adult specimen, apical view; Figure 3: adult specimen, apertural view; Figure 4: adult specimen, lateral view; Figure 5a: juvenile specimen, apertural view; Figure 5b: apex of same specimen, showing micro-ornament; Figure 6a: adult specimen, apertural view; Figure 6b: micro-ornament at beginning of body whorl of same specimen; Figure 7: adult specimen, lateral view; Figures 8, 9: juvenile specimens, apertural views.

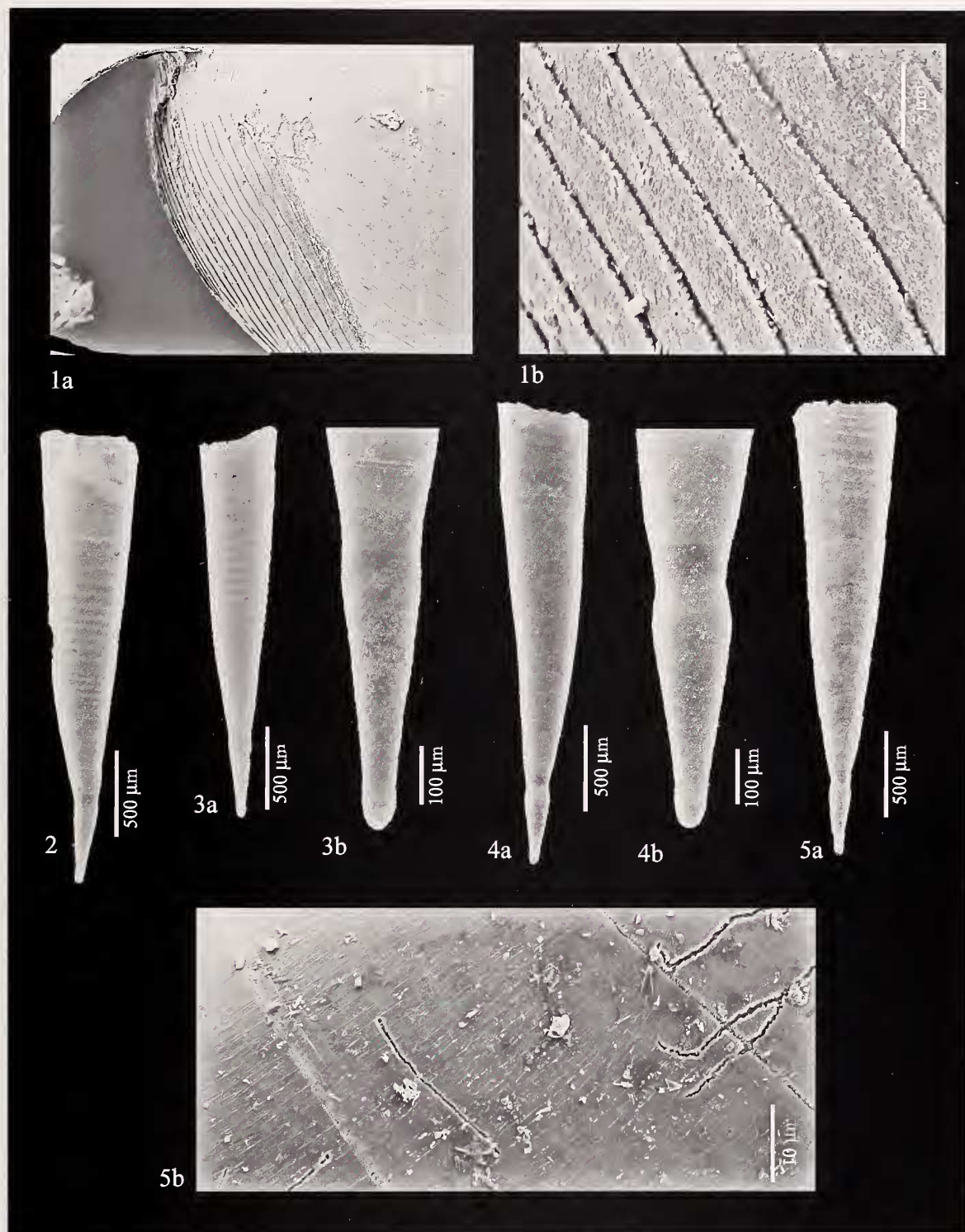


Plate 16. SEM-images of *Limacina trochiformis* (d'Orbigny 1836) (Figure 1, Red Sea, sample 14, RGM 540.418), *Creseis chierchiae* (Boas, 1886) (Figure 2, 3, Red Sea, sample 7, RGM 540.419; sample 11, RGM 540.420) and *Creseis chierchiae* (Boas, 1886) forma *constricta* Chen & Bè, 1964 (Figure 4, Gulf of Aden, sample 15, RGM 540.421; Figure 5, Red Sea, sample 7, RGM 540.422). Figure 1a: palatal side of aperture, showing radial ridges; Figure 1b: same specimen, radial ridges enlarged; Figure 2: adult specimen, ventral view; Figure 3a: adult specimen, lateral view; Figure 3b: same specimen, protoconch enlarged; Figure 4a: adult specimen, lateral view; Figure 4b: same specimen, protoconch enlarged; Figure 5a: adult specimen, dorsal view; Figure 5b: micro-ornament of same specimen.



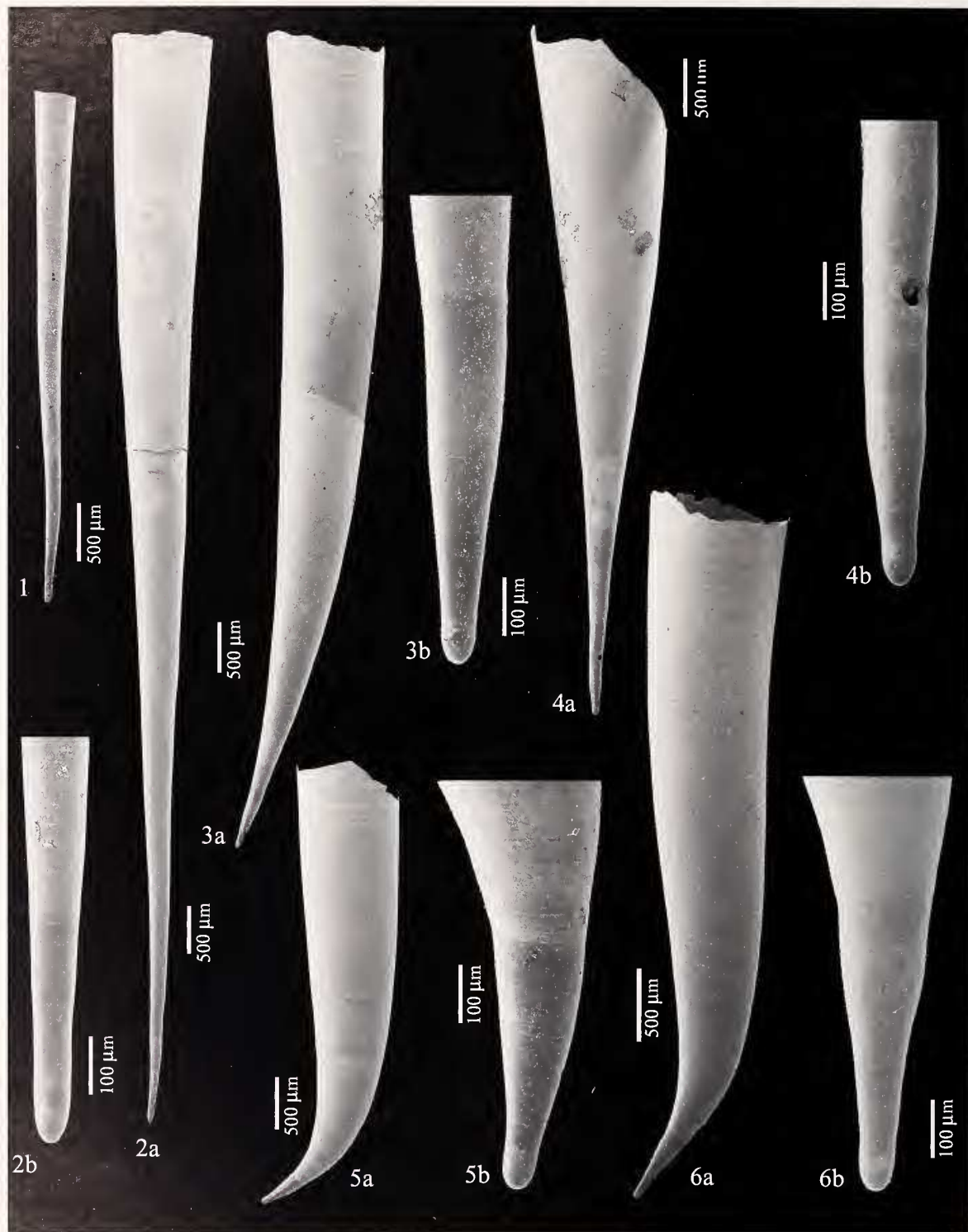


Plate 17. SEM-images of *Creseis claya* (Rang, 1828) (Figures 1, 2, Red Sea, sample 11, RGM 540.423–540.424); *Creseis conica* Eschscholtz, 1829 (Figures 3, 4, Red Sea, sample 13, RGM 540.425–540.426) and *Creseis virgula* (Rang, 1828) (Figures 5, 6, Red Sea, sample 12, RGM 540.427–540.428). Figure 1: semi-adult specimen; Figure 2a: adult specimen; Figure 2b: protoconch of same specimen, enlarged; Figure 3a: adult specimen, curved form; Figure 3b: protoconch of same specimen, enlarged; Figure 4a: adult specimen, straight form; Figure 4b: protoconch of same specimen, enlarged; Figure 5a: adult specimen, lateral view; Figure 5b: protoconch of same specimen, enlarged; Figure 6a: adult specimen, slightly flexuous form; Figure 6b: protoconch of same specimen, enlarged.

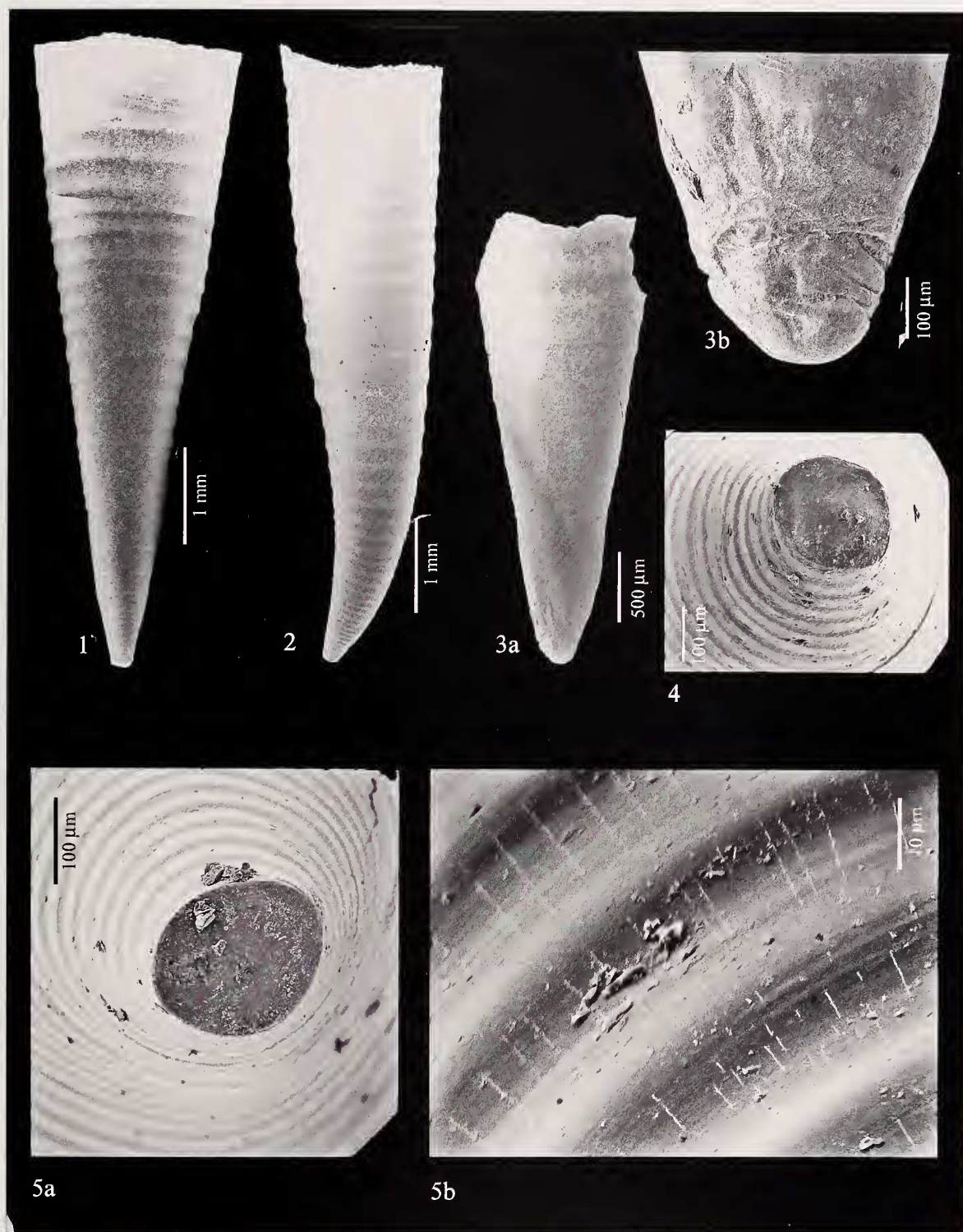


Plate 18. SEM-images of *Hyalocyclus striata* (Rang, 1828) (Figures 1, 2, Red Sea, sample 7, RGM 540.429–540.430; Figures 3, 4, Gulf of Aden, sample 15, RGM 540.431–540.432; Figure 5, Red Sea, sample 7, RGM 540.433). Figure 1: adult specimen, dorsal view; Figure 2: adult specimen, lateral view; Figure 3a: specimen with wrinkled apical portion; Figure 3b: apical portion, enlarged; Figure 4: apical view, showing septum; Figure 5a: apical portion, showing septum; Figure 5b: micro-ornament between annulations.



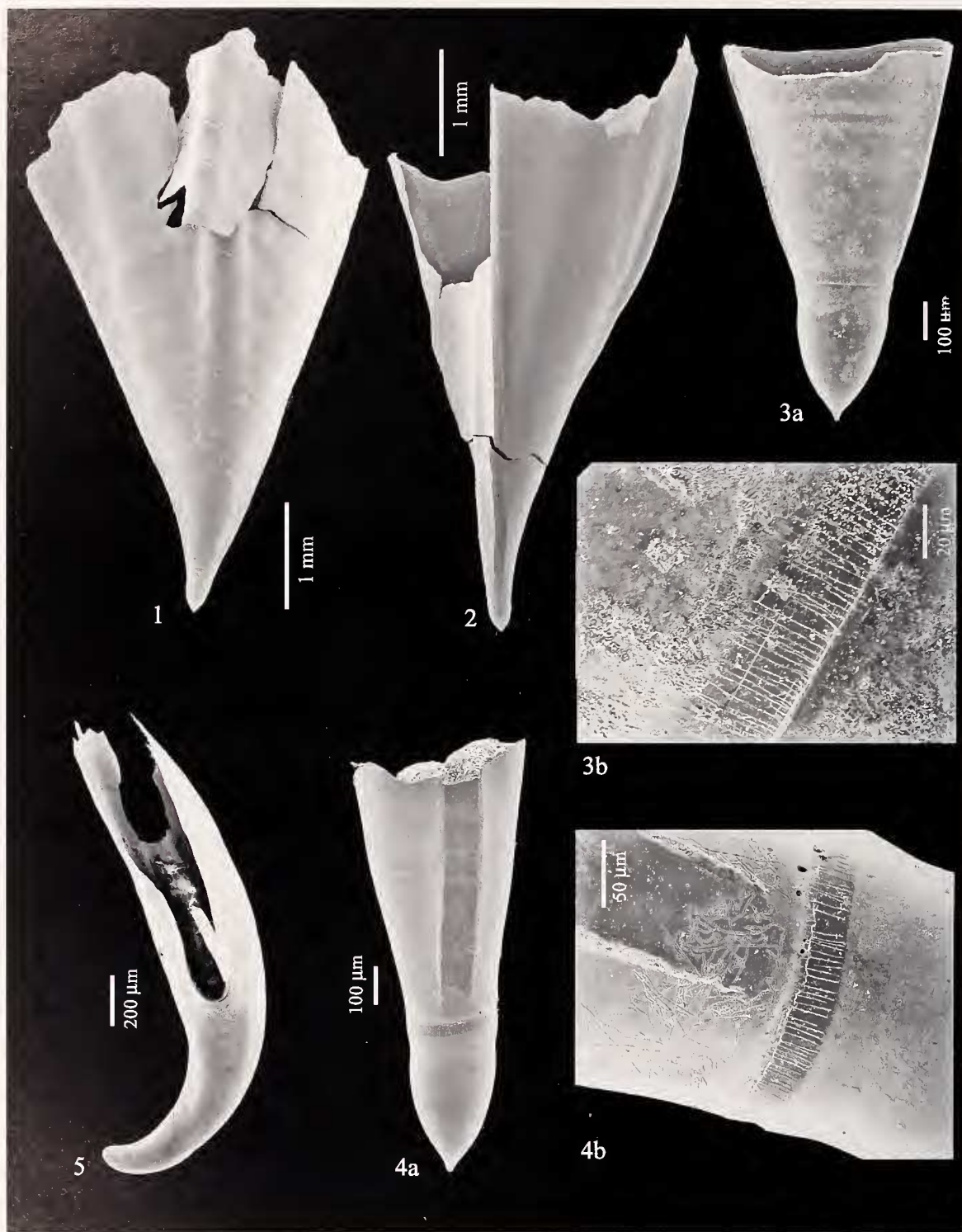


Plate 19. SEM-images of *Clio* (*Clio*) *convexa cyphosa* Rampal, 2002 (Figures 1, 2, Red Sea, sample 12, RGM 540.434–540.435; Figures 3, 4, Gulf of Aden, sample 15, RGM 540.436–540.437) and Cavoliniidae sp. (Figure 5, Red Sea, sample 11, RGM 540.438). Figure 1: adult specimen, dorsal view; Figure 2: adult specimen, left lateral view; Figure 3a: juvenile specimen, ventral view; Figure 3b: same specimen, showing radial micro-ornament on the boundary of protoconch and teleoconch; Figure 4a: juvenile specimen, right lateral view; Figure 4b: same specimen, showing micro-ornament on the boundary of protoconch and teleoconch; Figure 5: juvenile specimen, right lateral view.

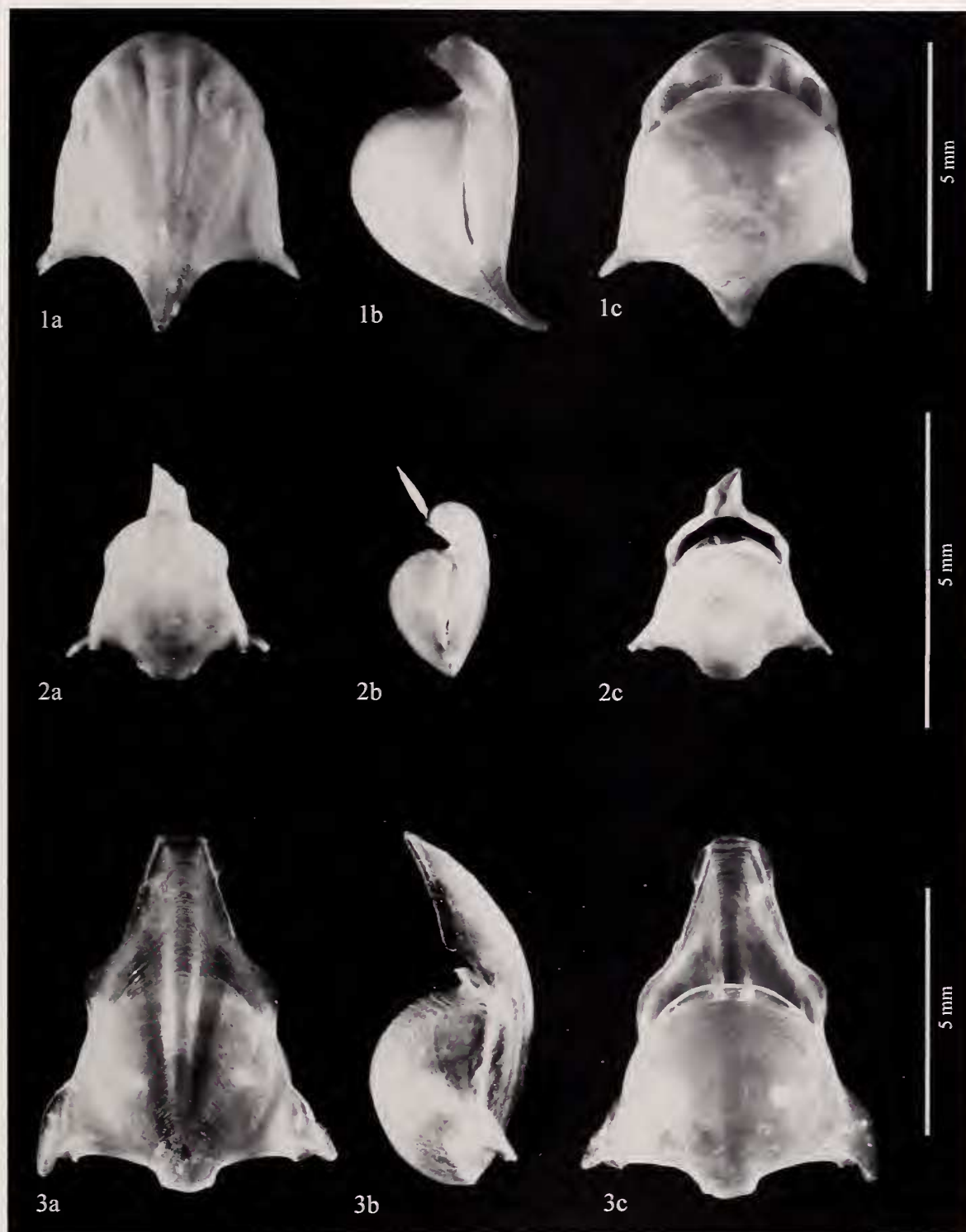


Plate 20. Photographs of *Cavolinia uncinata* (Rang, 1829) (Figure 1, Red Sea, sample 6, RGM 540.439), *Diacavolinia angulata* (Souleyet, 1852) (Figure 2, Gulf of Aden, sample 15, RGM 539.947) and *Diacavolinia flexipes* van der Spoel, Bleeker & Kobayashi, 1993 (Figure 3, Red Sea, sample 12, RGM 540.440). Adult specimens, a: dorsal view, b: left lateral view, c: ventral view.



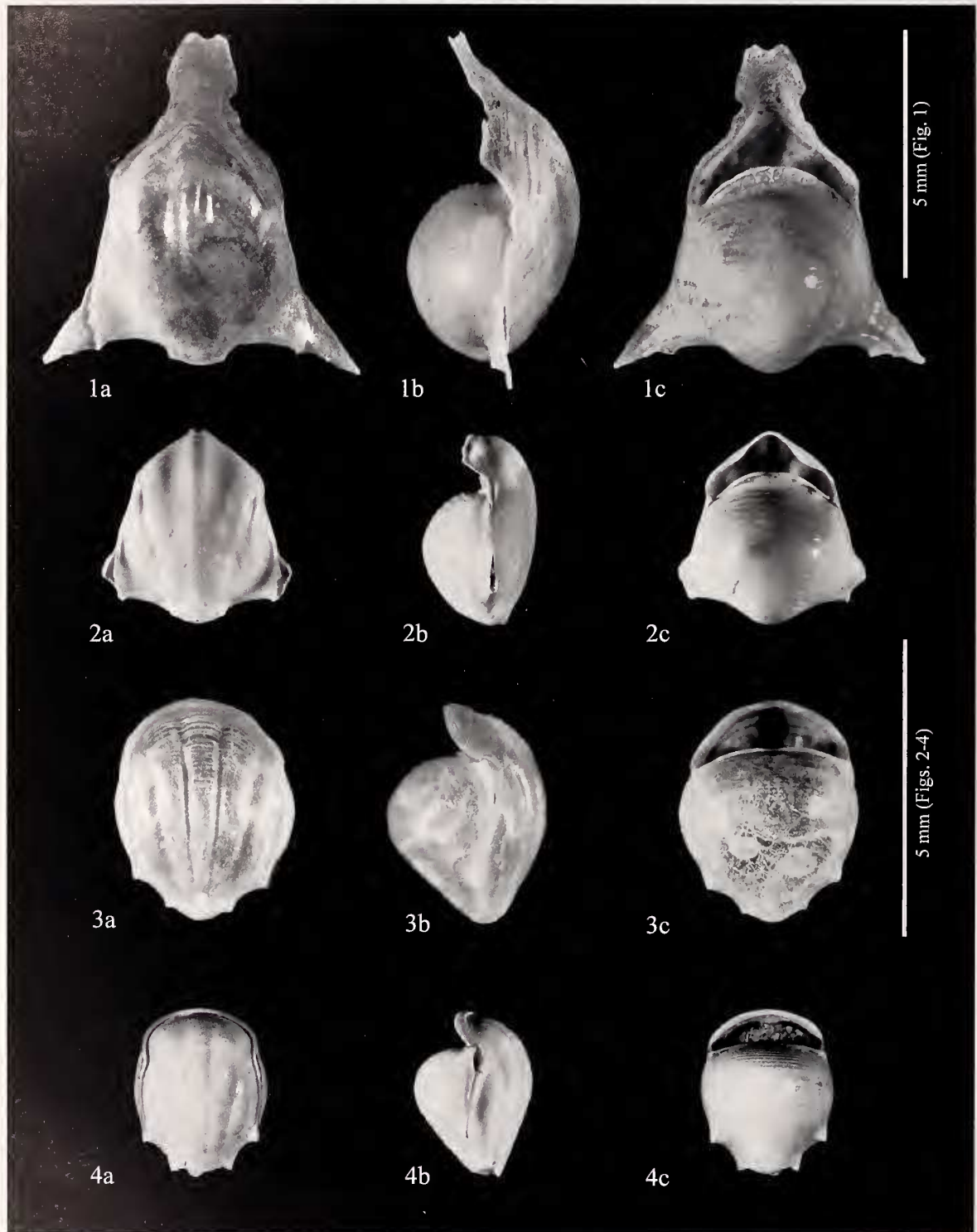


Plate 21. Photographs of *Diacavolinia longirostris* (de Blainville, 1821) (Figure 1, Gulf of Aden, sample 15, RGM 540.441); *Diacavolinia* sp. (Figure 2, Gulf of Aden, sample 15, RGM 540.442); *Diacria erythra* van der Spoel, 1971 (Figure 3, Red Sea, sample 12, RGM 540.443); and *Diacria quadridentata* (de Blainville, 1821) (Figure 4, Gulf of Aden, sample 15, RGM 540.444). Adult specimens, a: dorsal view, b: left lateral view, c: ventral view.

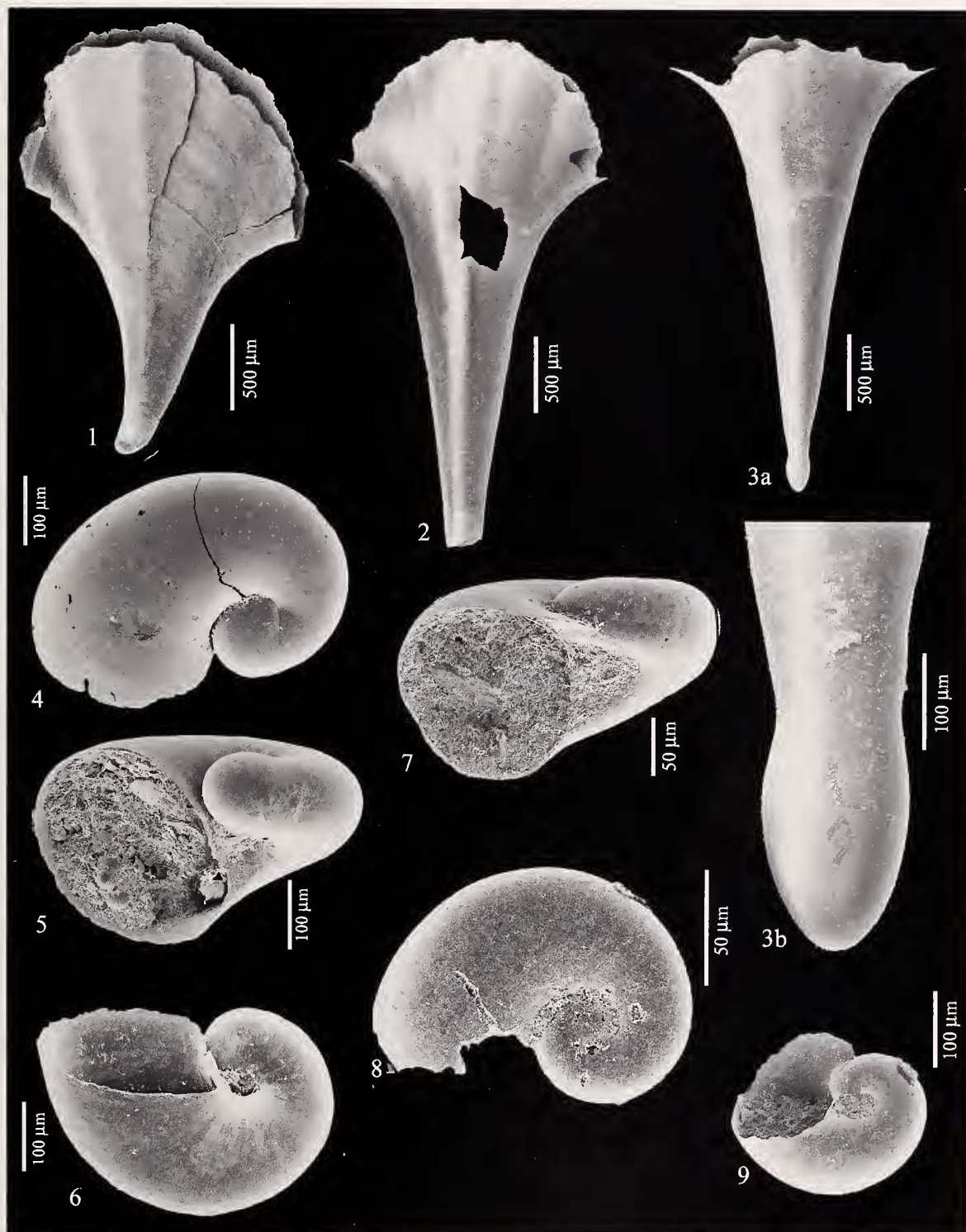


Plate 22. SEM-images of Cavoliniidae (Figure 1, Red Sea, sample 11, RGM 540.445), *Diacria erythra* van der Spoel, 1971 (Figures 2, 3, Red Sea, Sample 7, RGM 540.446–540.447), *Cymbulia* sp. 1 (Figures 4–6, Red Sea, sample 13, RGM 540.448–540.450) and *Cymbulia* sp. 2 (Figures 7–9, Red Sea, sample 7, RGM 540.451–540.453). Figure 1: juvenile specimen, dorsal view; Figure 2: juvenile specimen, protoconch broken, dorsal view; Figure 3a: juvenile specimen with protoconch, dorsal view; Figure 3b: same specimen, protoconch enlarged; Figure 4: larval shell, apical view; Figure 5: larval shell, apertural view; Figure 6: larval shell, apical view; Figure 7: larval shell, apertural view; Figure 8: larval shell, apical view; Figure 9: larval shell, umbilical view.



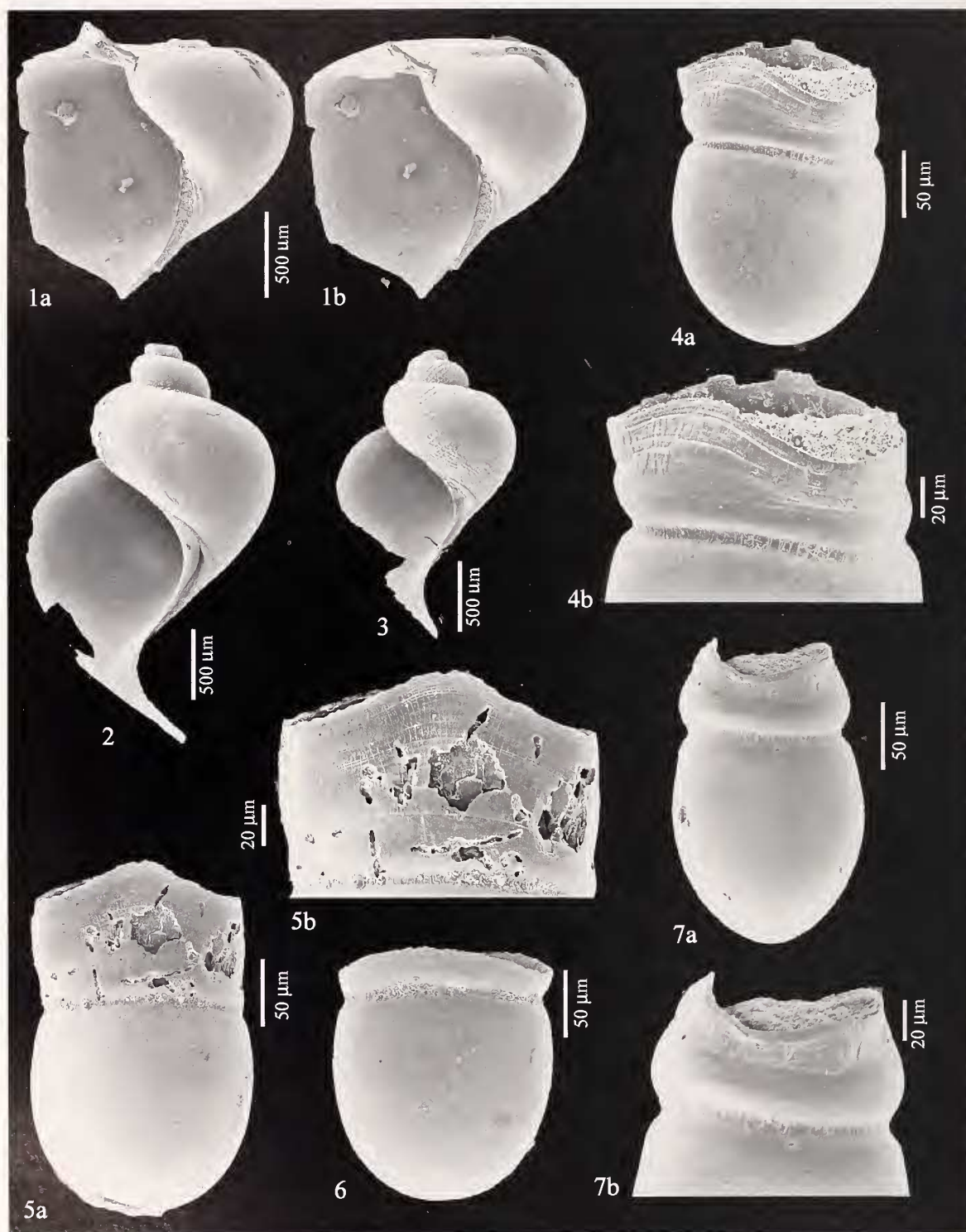


Plate 23. SEM-images of *Perachis moluccensis* Tesch, 1903 (Figure 1, Gulf of Aden, sample 15, RGM 540.454), *Perachis reticulata* (d'Orbigny, 1836) (Figure 2, 3, Red Sea, sample 12, RGM 540.455; sample 7, RGM 540.456) and *Gymnosomata* sp. 1 (Figures 4, 6 and 7, Red Sea, sample 13, RGM 540.457–540.459; Figure 5, Gulf of Aden, sample 15, RGM 540.460). Figure 1a: juvenile specimen, apertural view; Figure 1b: same specimen, oblique apertural/apical view; Figure 2: adult specimen, apertural view; Figure 3: adult specimen with remnants of reticulate eutieleum, apertural view; Figure 4a: larval shell, oblique frontal/lateral view; Figure 4b: same specimen, apertural part enlarged; Figure 5a: larval shell, frontal view; Figure 5b: same specimen, apertural part enlarged; Figure 6: larval shell, with early teleoconch (?) not developed; Figure 7a: larval shell, lateral view; Figure 7b: same specimen, apertural part enlarged.

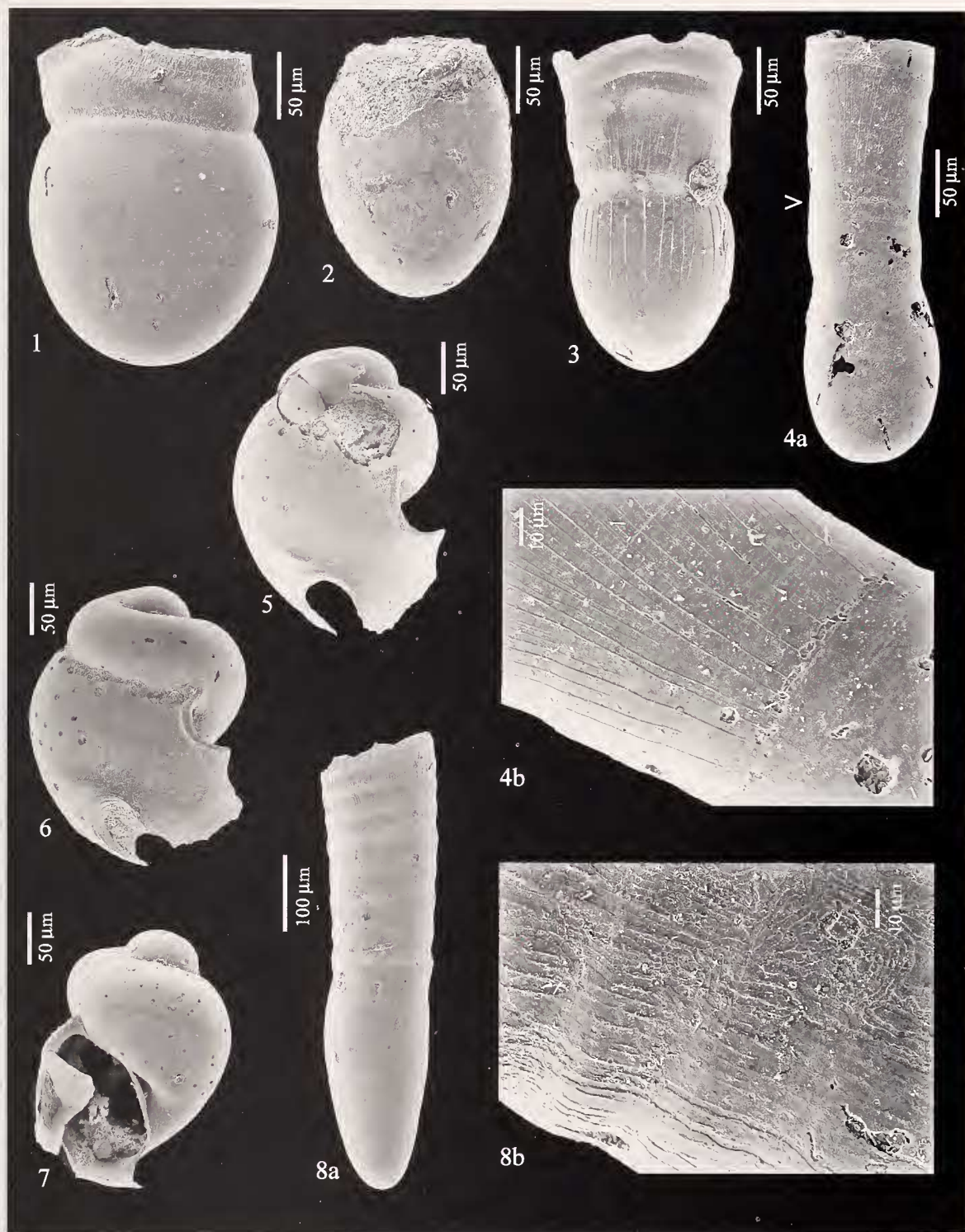


Plate 24. SEM-images of *Gymnosomata* sp. 1 (Figure 1, Red Sea, sample 7, RGM 539.895), *Gymnosomata* sp. 2 (Figure 2, Red Sea, sample 7, RGM 540.461), *Gymnosomata* sp. 3 (Figure 3, Red Sea, sample 13, RGM 539.897), *Gymnosomata* sp. 4 (Figure 4, Red Sea, sample 13, RGM 539.992), veliger larva of unknown gastropod (Figures 5–6, Red Sea, sample 7; RGM 540.462–540.463; Figure 7, Red Sea, sample 13, RGM 540.464) and 'beaked larva' *sensu* van der Spoel & Newman, 1990 (Figure 8, Red Sea, sample 7, RGM 539.898). Figure 1: larval shell, frontal view; Figure 2: larval shell, damaged, frontal view; Figure 3: larval shell, frontal view; Figure 4a: larval shell, frontal view (> indicates the boundary between protoconch-2 and early teleoconch); Figure 4b: same specimen, micro-ornament of longitudinal ridges on early teleoconch; Figures 5, 6: larval shell, lateral views; Figure 7: larval shell, apertural view; Figure 8a: protoconch and early shell parts; Figure 8b: micro-ornament on early shell part beyond protoconch.



as a reinforcement. These structures resemble some veliger larvae of benthic gastropods, but none of the many available specimens demonstrates a further development beyond the apertural protoconch margin. The sinistral coiling of the shells suggests an opisthobranch species. Very similar, if not identical, specimens in phosphoritic internal mould preservation are available from the Miocene of Malta (RGM collections).

'Beaked larva' *sensu* van der Spoel & Newman, 1990

Pl. 24, fig. 8a, b

1990 Beaked larva—van der Spoel & Newman, p. 207, fig. 5 (and references therein).

Discussion—A single, incomplete specimen was collected from sample 7. Although it shows resemblances with some of the Gymnosomata discussed above it seems to represent a specimen of what was called 'beaked larva' by van der Spoel & Newman (1990). The shape of the elongately oval initial shell part and the annulations on the younger shell part agree completely. This latter part also bears a somewhat irregular longitudinal micro-ornament (Pl. 24, fig. 8b). The apertural shell parts with the structures, described by van der Spoel & Newman, are missing in this specimen.

## RESULTS

The present study leads to conclusions about the actual holoplanktonic mollusc stock in the Red Sea. As all material is from bottom samples no living specimens were seen. In practically all cases, however, the samples contain fresh specimens the age of which, as demonstrated by von Rützen-Kositzkau (1999: 49) is no more than maximally ~6 kA. It is assumed that all species found in the bottom samples do occur alive at the present day.

Only epi- and mesopelagic species were found. Bathypelagic species are absent. Weikert (1982, tab. 3) found a strong reduction of pteropod abundances below 750 m sea depth, and related this phenomenon to high temperature and salinity, together with strongly reduced oxygen contents and a lack of food. Weikert (1987) found the lowest oxygen contents between 200 and 640 m, increasing again below 750 m.

A clear distinction can be made in a first group of species occurring all over the Red Sea, a second group only occurring in the southeastern part, and a third group occurring in the Gulf of Aden, but absent in the Red Sea proper. These groups are specified in Table 3.

All pteropod species recorded from the Gulf of Aqaba and the northernmost Red Sea by Almogi-Labin (1984, p. 495) occur also in group 1 (Table 3). Some species of group 1, however, according to her data have not reached the Gulf of Aqaba, *viz.* *Creseis*

*chierchiae* f. *constricta* and *Hyalocypris striata*, which is acknowledged by my results (Table 2). The same is true for several further species, as indicated in Table 3. Earlier records (Almogi-Labin & Reiss, 1977) of '*Cuvierina columnella urceolaris*' and *Clio polita* are corrected by Almogi-Labin (1984) as respectively 'a gastropod' (but in reality is a siphonodentaliid scaphopod) and 'a gymnosomate pteropod' (most probably identical with *Gymnosomata* sp. 1 in the present paper).

Species in group 2 obviously do not tolerate the stress of northward increasing salinity. High temperature cannot be a factor here, as it decreases in northern direction. The same tendency is visible in some species of group 1 that, although present all over the Red Sea, show distinctly decreasing numbers of specimens per sample in northwestern direction, *viz.* *Atlanta turriculata*, *Creseis chierchiae* f. *constricta*, *Hyalocypris striata* and *Diacavolinia flexipes*. All specifically identified Group 3 species, absent in the Red Sea, but found in the Gulf of Aden sample, have a wider distribution in the Indian Ocean, but most of them occur in low numbers, indicating that already in the Gulf of Aden the environment is less favourable than in more open oceanic surroundings.

This latter statement is also indicated by species present in the open Indian Ocean (albeit sometimes rare), but not found in the Gulf of Aden sample, such as *Atlanta gaudichaudi* Souleyet, 1852, *A. gibbosa* Souleyet, 1852, *A. inflata* Souleyet, 1852, *A. meteori* Richter, 1972, *Protatlanta souleyeti* (Smith, 1888), several Carinariidae (which may be represented, however, by unidentified larval shells, see Carinariidae spp. 1–3, above) and Pterotracheidae species, *Cuvierina urceolaris* (Mörch, 1850), *Cavolinia globulosa* (Gray, 1850), *C. inflexa* (Lesueur, 1813) and *Peraclis apicifurva* (Meisenheimer, 1906) (most data from Richter, 1974, 1979, 1993). Van der Spoel's (1976) distribution maps additionally indicate the occurrence of the following gymnosomatous species in the NW Indian Ocean: *Pneumodermopsis paucidens* (Boas, 1886), *Pneumoderma mediterraneum* (van Beneden, 1838), *Pruvotella pellucida* (Quoy & Gaimard, 1832), *Thliptodon diaphanus* (Meisenheimer, 1902), *Cliopsis krolini* Troschel, 1854, and *Paraclione longicaudata* (Souleyet, 1852). The specimens here indicated as *Gymnosomata* spp. potentially can belong to these taxa.

*C. inflexa* was recorded from the Gulf of Aqaba by Yaron (1977, p. 75) and from the Red Sea by Weikert (1982, p. 136). As that species is absent from all samples studied here I consider these records doubtful, their identification has to be checked.

A single specimen of '*Cuvierina columnella* (Rang, 1827)' was recorded from the Red Sea by Bandel & Hemleben (1995, p. 235, fig. 6E). Most probably this was a 'lost' specimen of *C. urceolaris* (Mörch, 1850), compare

Table 3

Holoplanktonic mollusc species found in the present study distributed all over the Red Sea (group 1, \* = also Gulf of Aqaba), only in the southeastern part of the Red Sea (group 2) and absent from the Red Sea, but present in the Gulf of Aden (group 3).

Group 1	Group 2	Group 3
<i>Atlanta fusca</i>	<i>Atlanta echinogyra</i>	<i>Oxygyrus keraudreni</i>
<i>Atlanta helicinoides</i>	<i>Atlanta frontieri</i>	Carinariidae sp. 2
* <i>Atlanta inclinata</i>	<i>Atlanta lesueuri</i>	<i>Styliola subula</i>
<i>Atlanta oligogyra</i>	<i>Atlanta plana</i>	<i>Clio pyramidata</i> f. <i>lanceolata</i>
<i>Atlanta turriculata</i>	Carinariidae sp. 1	<i>Diacavolinia angulata</i>
* <i>Heliconoides inflata</i>	Carinariidae sp. 3	<i>Diacavolinia longirostris</i>
<i>Limacina bulimoides</i>	<i>Firoloida demarestia</i>	<i>Diacavolinia</i> sp.
* <i>Limacina trochiformis</i>	<i>Janthina</i> sp.	<i>Diacria quadridentata</i>
<i>Creseis chierchiaie</i> f. <i>constricta</i>	<i>Creseis chierchiaie</i>	<i>Diacria trispinosa</i>
* <i>Creseis clava</i>	<i>Creseis conica</i>	<i>Peraclis moluccensis</i>
* <i>Creseis virgula</i>	<i>Clio cuspidata</i> ?	
<i>Hyalocyclus striata</i>	<i>Cymbulia</i> sp. 2	
* <i>Clio convexa cyphosa</i>	Gymnosomata spp. 1–4	
* <i>Cavolinia uncinata</i>		
* <i>Diacavolinia flexipes</i>		
* <i>Diacria erythra</i>		
<i>Cymbulia</i> sp. 1		
<i>Peraclis reticulata</i>		

the distribution map in Janssen (2005, fig. 35). Their illustration only shows the apical shell part with septum.

Dekker & Orlin (2000, p. 24) listed 5 species of Atlantidae for the Red Sea, of which, however, *Atlanta peroni* was not encountered during the present study. *A. brunnea* Gray, 1850, mentioned by these authors, is a synonym of *A. fusca*. Additionally, they refer (p. 25) to 5 species of Janthinidae (see above for a discussion) and (p. 35) to 13 taxa of Thecosomata, of which, however, the species *Cavolinia inflexa*, *C. tridentata* (Niebuhr, 1775), *Clio pyramidata* Linné, 1767 and *Styliola subula* do not belong to the actual Red Sea fauna. *Desmopterus papilio* Chun, 1889 and one gymnosomatous species, *Pneumoderma peronii* (Lamarck, 1819), mentioned for the Red Sea by these authors, were not recognised in the present sample material, but may have been based on live specimens from plankton hauls. *C. tridentata* was recorded from the Gulf of Aqaba by Barash & Zenziper (1994, p. 58), but not illustrated. I consider that a very doubtful record.

Professor Klaus Bandel (Geologisches Institut, Universität Hamburg, Germany) (in litt., 2006) noted the common presence of the (more or less) holoplanktonic nudibranch *Glaucus atlanticus* Forster, 1777 (superfamily Aeolidioidea Gray, 1827, family Glaucidae Gray, 1827) in plankton hauls of the southern Red Sea, but did not include this record in Bandel et al. (1997), as their reproduction could not be studied.

## FOSSIL OCCURRENCES

Several species not found during this study in the Red Sea were recorded as fossils from that area in literature. Chen (1969) distinguished four layers in late-pleistocene and holocene hot brine sediments (covering c. 70 kA) containing pteropods, of which only some are mentioned, all of these also occurring in the present samples. Berggren (1969) summarised his results, and compared them to other disciplines.

Herman (1971, tab. 35.8) found, among other species, *Cavolinia inflexa* from northern Red Sea postglacial cores and *Diacria trispinosa* in cores from several last glacial stages. In her tab. 35.9 she referred to other species, viz. *Cavolinia globulosa* and *Clio pyramidata*. The actual presence of the former of these two in the Red Sea was acknowledged only by Rampal (1985; see above).

Almogi-Labin (1982) found *C. inflexa*, *D. trispinosa*, *Styliola subula* and a *Peraclis* species different from *P. reticulata* in the Pleistocene marine isotope stage 5. *Hyalocyclus striata* is in that paper also recorded from the Gulf of Aqaba as a holocene/pleistocene fossil. Similar data on holocene/pleistocene fossils are given by Almogi-Labin (1986) and Almogi-Labin et al. (1998). A specifically unidentified *Peraclis* species, occurring next to *P. reticulata*, was also recorded by Rampal (1985).

Ivanova (1985) studied Late Quaternary biostratigraphy and paleotemperatures in cores from the Red



Sea and Gulf of Aden. From her stratigraphic interval-I in the Red Sea, comprising the last 11 kA, this author recorded the species *Styliola subula*, *Cavolinia inflexa* and *Diacria trispinosa*, species presently no more occurring in the Red Sea fauna. For the Gulf of Aden she recorded an additional species, not found in my Gulf of Aden sample, viz. *Limacina lesneuri* (d'Orbigny, 1836). *Gymnosomata* sp. 1 is recorded by her from almost all samples (intervals I–V, comprising c. 100kA), but misidentified as *Clio polita* (Pelseneer). It is only absent in her interval-I sample from the Gulf of Aden. *Clio pyramidata* was only recognised in core samples from outside the Red Sea.

Almogi-Labin et al. (1986) studied pteropod shell preservation in a core from the northern Red Sea in relation to stable isotope ratios of carbon and oxygen. They found generally well-preserved shells during glacial stages, and deteriorating preservation during interglacials, with in extreme cases complete dissolution of the aragonite. A last occurrence peak of internal moulds (with or without aragonitic shell) they found at a depth of 0.50 m below sea bottom (lower part of 'Stage 1'). It is supposed that this level was also reached by the boxcores in samples 3 to 6 of the present study. These results led to the application of pteropods as palaeoclimate indicators (Almogi-Labin, 1984; Almogi-Labin et al., 1991, 1998; Hemleben et al., 1996). In a core from the central Red Sea Almogi-Labin et al. (1998, p. 94, fig. 5) found no pteropod moulds and only very few moulds with the original shell preserved. This agrees with the present samples 7–15, in which no internal moulds were observed.

Final note—A further cavoliniid taxon, *Cavolinia gibboides* Rampal, 2002, was recently separated from the well-known species *C. gibbosa* (d'Orbigny, 1836) on the basis of predominantly morphometric characteristics. Its distribution is given as 'en Méditerranée orientale et en Mer Rouge septentrionale (Golfe d'Aqaba)' (Rampal, 2002, p. 221, fig. 4R). In the absence of material for comparison I so far have no well-considered opinion on the validity of the name *C. gibboides*, but there are two reasons making me believe that this species does not occur in the Gulf of Aqaba. First, in the material available for this paper nothing similar to the *C. gibbosa*-group was found to be present, and second, in the specification of material studied by Rampal (pp. 220–221), under the sub-heading 'Golfe d'Aqaba,' only samples from Cyprus are mentioned. This makes me believe that the Gulf of Aqaba occurrence is erroneous.

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